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THE CEREBELLUM

AN INVESTIGATION OF RECENT
ADVANCES

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FREDERICK TILNEY, M.D.
THOMAS K. DAVIS, M.D.
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PREFACE

This volume is Number Six in the series published by the Association for Research in Nervous and Mental Disease. The meeting whose transactions it reports was devoted to the subject of the cerebellum. Investigators from all parts of the country contributed original studies covering most of the important aspects of this field. Certain features of the subject were not dealt with as extensively as might be desired and it is hoped that these deficiencies will be corrected at a subsequent meeting of the Association.

In presenting the material, the Editorial Board has endeavored to follow in so far as possible, the general plan adopted for previous meetings, giving the original contributions in extenso as well as a verbatim report of the questions presented by the Commission and the answers made by the several authors. Both question and answer have been somewhat freely edited to avoid repetitions or lack of clearness, but in all cases the copy containing such correction has been submitted for approval to the Commission and to the contributors.

The Editorial Board feels deeply indebted for the kind and effective coöperation of all the authors and to the members of the Commission who have been of great service in their advice and suggestions. The editors are particularly desirous of expressing their appreciation to Dr. T. H. Weisenburg who has been at no little pains in providing publication of the original articles in the *Archives of Neurology and Psychiatry*.

F. T.

May 25, 1929.

Section I
MORPHOLOGY

CHAPTER I

UNSOLVED PROBLEMS SUGGESTED BY CEREBELLAR CONNECTIONS AND CEREBELLAR HISTOLOGY

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THE neurological sciences have never experienced, probably, the dissociation between the anatomic and physiologic points of view which is so bitterly complained of elsewhere in the present dynamic welter. Consequently, probably, everyone who has been occupied with neuro-anatomic problems has always sought to interpret his findings more or less in terms of function as well. The present paper aims to voice, so to speak, the obstacles of such functional interpretation which are due to lacunae in our knowledge of neuroanatomy and of which probably nearly everyone working in this line is aware. Hence the banal character of these few reflections—at least to neuro-anatomists. It may be that before this paper is read some of the questions raised will have received their answers.

Broadly speaking, in dealing with the central nervous system as a whole or with any portion of its gray matter or even with any individual neurone, three questions arise: (a) what are the sources of the nerve fibers terminating in the structure in question, whether it be the whole central nervous system, certain masses of gray or single neurones, and what kind of nerve impulses do they convey to it; (b) what does the structure itself do to these impulses; and, finally, (c) what is the distribution of the fibers emerging from it and what is the ultimate distribution and effect of the efferent impulses conveyed by such fibers.

Investigations of the nervous system, whether anatomic or physiologic, must always be an attack on some special portion of it or some particular function. This analytic approach has been criticized—both in neurology and other branches of science. We hear such statements as that the body, or the nervous system, or the cortex, “functions as a whole.” This statement may be quite true but irrelevant as a protest against analysis as a necessary preliminary to synthesis. It is,

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however, a good corrective to any tendency to regard the nervous system as a congeries of circuits acting independently of each other. The importance of the various integrations before the lowest levels are reached, so beautifully illustrated in Drs. Tilney and Riley's book, is better realized than formerly. Voluntary movements, for example, may partially disappear with pyramidal tract injury, but no one considers this tract as the sole carrier of all impulses necessary for the normal performance of such voluntary movements. How far lower reflex circuits can act independently, how far they maintain their independence with the increasing development of forebrain and correlated mechanisms and the nature of the influence of such higher centers upon them have always been fundamental problems in neurology. It would appear, however, that modification of the activity of one circuit by another would be accomplished mainly by some form of combination with the afferent impulses received by the modified center from other sources. More and more, too, there emerges the importance of afferent impulses adding constantly and (consequently?) not occupying the field of attention, such as the protopathic, especially visceral field whose dissociated activities have so occupied the attention of the psycho-analyst and the proprioceptive—especially the tonic proprioceptive—field so germane to cerebellar discussion.

Since Sherrington's work it has been customary to speak of the cerebellum as the great proprioceptive "ganglion" or coördinating center. That this statement throws great light upon the nature of the cerebellum is true, but—as will appear later—certain qualifications apparently must be made. This must not be taken to minimize the obvious but nevertheless very important truth that one great ultimate source of all impulses regulating—not necessarily initiating—all movement as well as tonus and that distribution of tonus known as posture must be the stimuli arising in the organs of movement and posture, the muscles and tendons themselves. In all the diverse normal reactions of the voluntary musculature to various stimuli, however coördinated by the central nervous system, this proprioceptive element must be present.

The following applies principally to mammals and especially to man:

Starting with the peripheral sources of afferent impulses to the cerebellum: Is this proprioceptive source established from the point of view of purely anatomic observations? It seems to me very prob-

able rather than absolutely proven. We have no degeneration experiments showing, *e.g.*, that neurones terminating peripherally in muscle-tendon spindles and perhaps other proprioceptors terminate centrally around Clarke's column. On the other hand, we have much evidence that many of the coarse fibers running up the dorsal column and giving offsets to Clarke's column originate from a certain type or types of larger spinal ganglion cells which in turn send their peripheral processes to proprioceptors. Along with these, in the dorsal column, however, are probably fibers from the corpuscles of Pacini and Meissner, the latter probably carrying tactile impulses. There has at present, as far as I am aware, been no differentiation made between these categories as regards termination in Clarke's column—or indeed elsewhere. So while it is highly probable that the fibers ending in Clarke's column are in part proprioceptive (position and movement), there is no strict anatomic proof that other kinds of impulses may not also be received. It may be remarked that the writer has never seen any basis for assigning to Clarke's column or to the cerebellum any visceral function. Also that while the term proprioceptive is useful, it has likewise led to confusion. The same applies to the term autonomic. The writer confesses that he is uncertain as to the exact meaning of these terms in Winkler's great work. Would it not be better, in protocols of sensory examinations at least, to simply state the implement and *modus operandi* of the tests and not use terms of various categories of sensibility?

It is obvious from the above that there cannot be any proof as to the respective rôles played by the tendon and the muscle spindles. The interesting phenomenon—which I believe often occurs—that in a tenotomy, say of the Achilles tendon, the tendon reflex is lost but the sensation of movement and position retained would seem to indicate that the tendon and articular receptors mediate the reflex and the muscle spindles the sensation. Further observations might be made on this point.

Passing into the cord, we may note that, according to statements in some books, the fibers ending in Clarke's column are terminals of medium length ascending fibers. According to Cajal's observations, the fibers entering this column are principally not terminals but collateral branches. While it is important to verify in adult man many of the observations as to collaterals made by Golgi's method upon young or embryo mammals other than man, this observation of

Cajal's is in accord with the fact, easily seen in silver preparations of the adult human cord, that the fibers entering Clarke's column from the dorsal white column are of smaller caliber than the great majority of the fibers of the dorsal column. This being the case, it seems probable that some at least of the individual proprioceptive fibers entering the dorsal column may convey the stimuli traveling along them not only to Clarke's column and thence to cerebellum but to the nuclei of the dorsal columns and thence to thalamus and cortex; to which should be added collaterals for cord reflexes and possibly other destinations. Such facts have an interesting bearing upon the problems of timing, summation and also certain questions concerning determination of paths by least resistance. It is also evident that tabetic ataxia, especially if due to a radiculitis, is not a pure cortical, *i.e.*, sensory ataxia but a combined cerebellar and cortical plus perhaps other factors. The general functional rôle of collaterals is one of the fundamental problems of neuro-physiology.

Another question which arises is the question of localization in Clarke's column. The radicular lamination of the longer ascending root arms in the dorsal column is well known and is in fact almost a corollary of the invariable relation of entering roots to dorsal gray. The collaterals from entering root fibers, exclusive of those to the zone of Lissauer, appear to follow a general law necessitated, one might say, by the above arrangement. The collaterals given off first after entry naturally go through the gelatinosa into the plexus beyond, next those curving around its mesial side, and lastly those to the most mesial gray of the cord, *i.e.*, Clarke's column. One result of this is that, at any given level, the outer or lateral part of the column of Clarke receives collaterals from roots entering higher than those sending collaterals to its mesial part. That this is the case can be seen from a study of successive levels above a low cord crush. Just above the crush, the column of Clarke is destitute of entering dorsal column collaterals, higher, those from roots below begin to enter its lateral portion, still higher the mesial portion is filled in.

Another, perhaps more important, result of the easily made observation that the column of Clarke receives collaterals from the middle part of the dorsal column is that these fibers come from segments below the level of the entry of their collaterals into Clarke's column. When this is coupled with the fact that Clarke's column is well developed—in fact very large—in the twelfth thoracic segment it is

obvious that while the dorsal spino-cerebellar tract perhaps principally conveys trunk impulses to the cerebellum it also conveys impulses from the lower extremity. It would be interesting to ascertain whether this bears any relation either to the segmental innervation or the segmentary innervation of the lower extremity. If we assume that the fibers entering the lower part of Clarke's column are principally from the higher lumbar segments we reach the interesting conclusion that the cerebellum receives principally, as far as the lower extremity and dorsal spino-cerebellar tract is concerned, impulses from the thigh flexors and leg extensors. This conclusion, in view of the shortness of the lumbo-sacral segments, cannot be drawn with any degree of probability; *a priori*, in view of the trunkal character of the column of Clarke one would expect the proximal segment—the thigh—to be favored. In questions of this kind the descending arms of dorsal root fibers must also be taken into account.

Such considerations as the above, show how much is still to be done, especially on the human cord, in the finer analysis of its fiber systems. There is still need of detailed study of secondary cord degeneration resulting from definite lesions, in conjunction with clinical observations as far as possible and with the result recorded by careful level photographs rather than the prevailing simple line drawings; so that others can use them for other interpretations as well. It may be said in general that a comparison of figures in textbooks reveals a surprising amount of variation in the localization of the principal tracts with very little mention of level variations. A friend of mine once remarked that the surgeons are always looking for something to cut. This remark was made apropos of the section of the spino-thalamic tract to abolish painful sensations from certain parts of the body. In how many of these priceless lesions have their scientific possibilities been fully exploited? In how many of them have there been comprehensive and thorough pre- and post-operative sensory examinations? Are even clinical cases without operation or autopsy fully utilized? Some text-books speak of a second pain path, for deep pain, in the dorsal columns. A case was presented at a certain conference recently of a patient with loss of superficial pain in one lower extremity and part of the trunk on that side, slight opposite signs of pyramidal involvement and no disturbance of the sense of position and movement. Pressure pain and pain on extreme flexion and extension at joints (rarely tested, but important in such questions) were

also absent, clearly showing the improbability of any such dorsal column pain pathway.

From the above we gain a conception of a segmental arrangement of Clarke's column, each root termination occupying a certain segment separated from adjoining segments by oblique boundaries. Is there any arrangement in the dorsal spino-cerebellar tract? As is well known, Collier and Buzzard some time ago thought there was a lamination of this tract, the lower segment being dorso-lateral in the upper levels. This arrangement would not be in accordance with the general law of eccentricity of the longest fibers but the factor on which this law depends must be taken into consideration, *i.e.*, that the last fibers to join a system naturally lie next their gray of origin, which in the cord is in a general way within. The fibers, however, passing from Clarke's column to the tract in question take, in most cases, a directly lateral course to the ventral part of the dorsal spino-cerebellar area. This would naturally result in a mainly dorso-ventral lamination, the dorsal laminae in a higher level being composed of those fibers arising from the lower segments of Clarke's column. In sections below a cervical crush where there was "retrograde" or traumatic degeneration of ascending tracts, the fibers of this tract persisting—at some distance below the lesion—occupied the dorsal part of the tract. Inasmuch as the fibers most apt to resist the trauma would be those from cells most remote from the lesion, this observation would tend to show a dorso-ventral lamination. On the other hand, a lumbo-sacral crush showed a diffuse degeneration throughout the dorsal spino-cerebellar area in thoracic sections. It may be higher levels would have shown more evidence of lamination.

The ventral spino-cerebellar tract, both as to the location of its cells of origin, including their segmental location, appears to differ from the dorsal tract. To some extent, at least, it appears to fill out the deficiencies of the dorsal tract, especially as far as the neck (and limbs?) are concerned.

As shown by MacNalty and Horsley, and pointed out also by Kappers, the projection of the spino-cerebellars upon the cerebellar vermis does not agree very well with the fore and aft localization of head, neck, limbs, and trunk, there being a mixture of segmental representation. While this does not necessarily negative strict cerebellar localization entirely it still is adverse to it. Such observations are of great importance in other respects as bearing upon theories of cere-

bellar function and should be extended further. A careful study and comparison should be made of secondary degenerations following lesions at various levels of the human spinal cord. Such material can be collected and it may be pointed out that while only a short period—one to three weeks—after the incidence of the lesion is most favorable for Marchi preparations, the “Marchi bodies” remain a much longer period and would be available for work of this kind where finer fiber studies are not necessary. The importance of accurate information here is not solely as bearing upon localization but upon it hinges our general interpretation of cerebellar activity.

When we turn to bulbar afferent connections we find even more important gaps in our anatomic knowledge. Among the minor ones are the terminations in the cerebellum of the contingents from the nuclei of the lateral columns and from the external arcuate nuclei. Regarding the latter—and to some extent the former—we are also in ignorance as to the possible nature of the impulses they convey. Another interesting question, not much emphasized, is the termination of collaterals from spino-cerebellar fibers in bulbar lateral column and vestibular terminal nuclei and the giving off of collaterals from the olivo-cerebellar fibers. These points, some of which have been observed by Collier and Buzzard and others, have been stressed by Lorente de Nó who emphasizes the fact that all the various afferent proprioceptive fibers to the cerebellum thus establish lower circuits which may account for the compensation made possible thereby for the maintenance of the righting reflexes of Magnus-De Kleijn after destruction of the cerebellum. An important question is the moot one as to the connection of the nuclei of the dorsal columns with the cerebellum. The discrepancies here between observations on normal human brain stems and experimental work in other forms are well known. This may be explained possibly by Tilney's observations that the external or large-celled nucleus of von Monakow or Blumenau, or the external nucleus of the column of Burdach, may not be present in lower forms and may furnish such a connection in man. In connection with this it may be remarked that two apparently—but only apparently—antagonistic tendencies are emerging from comparative work, pioneered by C. L. Herrick and Edinger and now being carried on more intensively, especially here and in the Netherlands: first, the great light thrown upon the nature of the human central nervous system by such studies and second, the increasing revelation

of great differences between the central nervous systems of man and the usual experimental animals and the consequent great need of caution in applying *in toto* to man the results—especially physiological—obtained on such forms. Dr. Pike has always emphasized the great shifting of functional emphasis as we ascend to the anthropoids and man. There is a great need for much experimental work, both physiologic and anatomic, upon the anthropoids and still more utilization of human material. If only the craving of the general pathologist to carve the brain into unusable slices could be curbed or sublimated into a more careful macrotomy into more practical sections for future study this end might be more easily attained.

It seems fairly clear that the paleocerebellum receives proprioceptive stimuli from the organs of somatic movement via spino-cerebellar and probably certain afferent cranial nerve secondary tracts and also from that proprioceptive organ of the head—the vestibule. Regarding the latter, there is again uncertainty both as to whether and to what degree the cerebellum receives direct root fibers or secondary tracts, whether the projection is upon an internal nucleus, the nucleus fastigii, principally, or directly upon the cortex, and the exact distribution of vestibular impulses upon the cerebellar cortex. Allied unsettled points are concerning the variable striae medullares—now apparently not representing secondary cochlear tracts—together with the perpendicular fibers in the raphé, to which may be added those in the pons. Attention might be called here to the interesting but, to the writer, unsupported view of Winkler that Bechterew's nucleus is autonomic and also to the interesting Spanish observations showing the presence of efferent fibers in the cochlear root—but not from Bechterew's nucleus. There is also some uncertainty as to what proportion of the fibers connecting the bulbar vestibular field with the cerebellum are afferent and efferent, respectively.

In general, respecting these afferent paleocerebellar connections it may be remarked that while they are overshadowed in man by the more recent olivo- and ponto-cerebellar connections to the neocerebellum, they are still well developed and are only relatively to the latter insignificant.

It is when we come to the inferior olive, however, that a deficiency in our knowledge is revealed which, to my mind, bars the way to a clear anatomico-physiologic interpretation of the cerebellum. The distribution of the inferior olivary fibers upon the human cerebellar

cortex appears, thanks to the work of Holmes and Stewart, fairly well known and it is important to note that they apparently terminate in the vermis as well as hemispheres. It is also interesting to note a correspondence of certain parts of the nucleus with certain parts of the cerebellar cortex. This tendency to correspondence is marked in other connections such as the optic pathway and is especially striking in the topographic correspondence between the sensory paths from legs, arms and head in the bulb and in the cerebral hemispheres, the legs in both cases occupying the medial position. Such facts might furnish clues to those interested in the factors of histogenesis, not only in the nervous system but possibly elsewhere. In the above case of the sensory paths the correspondence appears to be one of the expressions of bilateral symmetry.

The great gap in our knowledge of the olivary connections is our ignorance of the source of the fibers ending in the olives. That the central tegmental tract and probably that of Helweg are the main, possibly only, afferent olivary connections is well established but the exact source of their fibers is not known. It must be remembered, though, that among the secondary ascending tracts in ventral and lateral cord, comprising fibers to bulb, paleo-cerebellum, tegmentum, colliculi, etc., are probably fibers to the olive, according to observations by Collier and Buzzard. These latter connections are old connections and it would be interesting to know if such spino-olivary fibers terminate only in the paleo-olive. On the other hand, as mentioned later, the tract of Helweg may be a newer acquisition.

The olives supply the vast majority of the fibers of the restiform body in man, they form one of the great cerebellar connections, they are mainly new structures but not as recent as the pontine connection, there being probably a paleoölive in all vertebrates, at least all with well developed cerebella; while they supply the vermis, their great development and linear convoluted character must be attributed in part at least to the necessity of covering in man the much larger hemispheres as well as the vermis. It is in connections of this kind that the necessity of concentrating upon the anthropoid and man is manifest. The comparatively insignificant olives of even such mammals as the cat do not lend themselves to their investigation by experimental methods. Whether the central tegmental tract is thalamic or tegmental in origin or both will probably be discussed by others but what a difference in interpretation according to what view is

held! It may be remarked in passing that it seems as though there should be some means of projecting ocular proprioceptive, in conjunction with retinal, impulses upon the cerebellum. As Magnus has shown, the optic righting reflexes increase in importance as we ascend the mammalian scale. On the other hand, if we accept a partial thalamic origin for this tract may it not represent the projection upon the cerebellum of the impulses necessary for the cerebellar regulation of various emotional and instinctive reactions performed by the somatic musculature as opposed to a pallial cerebellar control of the various voluntary muscular activities by the pallio-pontile system? It will be noted that this is contradictory to another speculative suggestion given below regarding the pallio-pontile systems.

If, as has been held by some, the olive receives fibers from the dorsal column nuclei, an ample spread from the whole body on the whole cerebellum might be provided for. This dorsal column-olivary connection should be crossed. In connection with this may be mentioned Tilney's conception that the olivo-cerebellar connection supplies the proprioceptive impulses for the cerebellar regulation of the neokinetic activities. This view certainly appeals to the writer and such a dorsal column-olivary connection would provide, perhaps, the ampler olivary connection which it would apparently require. If, on the other hand, the olivary connection should turn out to be one conveying impulses from such higher centers as thalamus and striatum, the whole neocerebellum would probably receive little or no direct proprioceptive stimuli. The importance of this question in cerebellar interpretation is obvious.

Does the topographic projection of the inferior olive upon the cerebellar cortex mean a similar topographic projection of the stimuli carried to it by this route? Obviously this question cannot be answered without a much more accurate knowledge of the afferent olivary systems such as the central tegmental tract. It must be pointed out here that absence of histologic evidence of isolated components in a conduction path does not necessarily militate against localization of stimuli traveling along it. There is no histologic evidence of such isolation in the nuclei of the dorsal columns of the cord yet in all probability stimuli traverse them which enable the pallial cortex to discriminate between two points about 2 mm. apart. Histology simply shows diffuse intermingled terminations of the dorsal column fibers in these masses of gray. This difficulty is solved if we

remember that, on the law of chances, no two terminals would hit the same aggregate of secondary neurones, some would be the same, many would not. There is no one-to-one neurone conduction, simply successive partial mixtures in successive nuclei but on the pallial cortex cutaneous point one must activate a somewhat different though probably overlapping aggregate of neurones from that activated by point two. As we see in the olivary, and especially in the visual path, there is some topographic representation but by overlapping groups in all probability. This general conception the writer owes partly to Doctor Casamajor, as emerging in a discussion of the question with him some time ago. The bearing of this conception upon questions of cerebral localization is obvious.

In the case of perception of movement and position, however, spatial discrimination is less important and what appears to be a varying intensity of stimulus seems to be the basis of the cortical discrimination. Here the tension of a whole muscle or muscles and attached tendons involves stimulation of many muscle-tendon receptors and the discrimination—cortical or otherwise—of the degree of tension and movement would apparently depend upon the intensity of their stimulation. Inasmuch as this apparently conflicts with the all-or-nothing principle, we must apparently, if we accept the latter centrally, resort to postulating the stimulation of an increasing number of receptors with increasing tension—much as the upholders of this theory account for varying degrees of tone and movement by the stimulation of varying numbers of muscle fibers by motor nerve fibers. These considerations would apply equally to the non-sensory proprioceptive projection upon the cerebellum.

When we turn to that still more recent and still more massive, in man, afferent cerebellar connection—the pallio-pontile or middle peduncular one—we have a more definite knowledge of the whole path in this case, from cortex cerebri to cortex cerebelli, but with important hiatuses. The first question is the important one as to whether the pontile fibers are distributed to the whole cerebellar cortex or whether all or part of the paleocerebellum (parts of vermis and flocculus) is exempted. There appears to be some difference of opinion here and it may be remarked again that this anatomic question should be determined in man, with his large pallial connection, as well as in lower forms. *A priori*, it would seem more probable that certain pallial impulses, especially those for standing, would be in-

tegrated with the afferent ones from the body by the paleo-cerebellar cortex but, as will be seen later, this integration may be performed elsewhere.

When we examine the pontile nuclei we find that not so much is known as to topographic representation in the cerebellar cortex as in the case of the inferior olive; not even in respect to the two great divisions of pallio-pontile fibers—frontal and temporo-parietal—terminating in them, though there is some evidence (Masuda) that there is such topographic representation and that the ponto-cerebellar continuation of the frontal tract is projected upon the caudal portion of the opposite cerebellar hemisphere and the temporal upon the cephalic. How can we get an anatomic clue as to the respective functions of these two divisions until their respective projections upon the cerebellar cortex have been determined? In general, the pontile nuclei would appear to have equal claim to topographic localization as the olive and yet it is not a laminar convoluted but a lump nucleus—an argument against the ultimate topographic character of the olive perhaps. The difference *may* be simply a matter of space accommodation.

While the general cortical origins of the pallio-pontile tracts are probably known, we appear to have very vague ideas as to their exact meaning. A careful study of the much neglected—by neurologists—*normal* infant might be helpful, combined with a study of myelogenesis. The order of development of higher centers concerned with movement apparently is first the older subcortical extrapyramidal systems, then the pyramids, and lastly the pallio-pontile systems. This seems to roughly coincide with the order of events to be observed in the infant: first the athetoid and other *normal* involuntary movements, then the definite attempts (pyramidal) to do something. These latter are poorly coördinated and uncertain, the uncertainty probably not merely due to imperfectly discriminated sensory impressions but to the imperfect action of the pallio-cerebellar mechanism. Incidentally, the normal infantile spastic grip, similar to that usually attributed to pyramidal lesions, may be mentioned and a further study of the postures of infants, both when asleep and awake, recommended. And what rôle does the earlier developing paleocerebellar, as distinguished from the neocerebellar, mechanism play at this stage of development? The defects of coördination, including standing, seen in certain defective children, probably fall partly under

this category. Granting, as seems to be the case, that the pallio-pontile projection is principally upon the neocerebellum, may it not be that these connections are principally simply to secure cerebellar coöperation in the more purely pallial, acquired, voluntary, pyramidal motor activities? Or should we say the more individualized and unilateral activities performed by the more recently acquired and increasingly important extremities, especially the hand? The view has been advanced that the temporo-parietal projection is especially in relation to a vestibular projection upon the cortex by presumably a vestibulo-collicular path. In this case the frontal might be assumed to be in relation to the great somatic muscle-tendon proprioceptive projection, though not in close spatial relations with it. The question of rubral connections should be considered in relation to this as will appear later. Pushing this line of thought further, may we not make another different distinction between the temporoparietal and frontal components? The relation of the former to possible vestibular centers has been emphasized by others, but might not this be extended to include a relation to all the surrounding sensory and gnostic areas? On the other hand, the frontal would have a relation perhaps to higher, more general and more synthesized motor manifestations including also, especially, emotional expression. The latter might in this case bear the same relation to the pallio-thalamic outflow that the temporo-parietal does to the pyramidal. The fact, however, that there is some evidence that the frontal has to do with standing—which would be in agreement with the above mentioned frontal projection upon caudal cerebellar hemispheres—does not fit in entirely with this view. Standing and the proper maintenance of the center of gravity in progression and other activities is enormously complicated, especially when simultaneously maintaining an upright posture, and requires a wide coördination of muscular adjustments—tonic as well as kinetic. The real antithesis of this would be the regulation of individual movements not so directly concerned in this latter maintenance. Further suggestions might be made, but what do we really know?

With the greatly increased interest in the subpallial extrapyramidal mechanisms there should be renewed study of the pallial ones. Without a clear comprehension of their activities there can be no complete grasp of the nature of pallial cortical activities in general.

Another obscure point which may be briefly mentioned is the existence of afferent, rubro-cerebellar, fibers in the superior peduncle.

When we look upon the afferent cerebellar connections broadly, while there is no definite evidence of precise topographic localization, the distinction formulated by Clarke and Horsley seems to hold good: that in general the middle, older portions of the cerebellum receive the more direct proprioceptive impulses from the body and head, especially from the older parts, *i.e.*, the trunk and head, and that there is also a distinction between the vestibular and other bodily areas; while the lateral newer portions receive more the olivary and especially the pontile impulses. In spite of this, while it appears to be true that injury to any of these connections causes the disturbances of movement and posture, ordinarily known as cerebellar ataxia, it is doubtful whether we at present can clinically differentiate the character of the disturbance due to each. When we consider the massive character of the pallio-ponto-cerebellar and olivo-cerebellar connections this inability seems almost pathetic.

It may be remarked, however, that clinical cases do appear to show a greater involvement of axial muscular mechanisms, or perhaps we should say of phylogenetically older bilateral movements, in vermis lesions.

It must be kept in mind, however, as shown later, that it is possible there are no marked differences clinically between the effects of lesions of the various afferent systems.

Before glancing at the cerebellar cortex, if we look at the efferent cerebellar connections we again find gaps which prevent a clear anatomico-physiologic comprehension of cerebellar activity.

That there are two principal outflows: one from the dentate, globose and emboliform nuclei *via* the superior peduncle and the other from the nucleus fastigii *via* juxtarestiform and uncinata fibers and thence, probably, principally by the various vestibulo spinal and vestibulo-mesencephalic tracts, seems fairly clear.

Regarding this latter connection, it is interesting to note that, judging especially by the work of Clarke and Horsley, it drains more than the vestibular cortex and possibly more than the spino-cerebellar areas as well. The question as to how far vestibular impulses are projected upon the cortex arises here. If they stop at the nucleus fastigii we have an interesting arrangement, *i.e.*, cortical integrations of another character acting upon this vestibular nucleus primarily. In any case the cerebellum appears in part to function as a higher circuit superimposed upon lower vestibular reflex circuits for carrying

other than vestibular integrations. The nature of this outlet would seem to point clearly to its being primarily for finer cerebellar vestibular integrations, using a common path with lower vestibular reflexes but at present, and possibly from the earliest period, apparently carrying out cerebellar integrations of other than vestibular material. If an early cerebellar control of purely lateral line and vestibular material were established, it might throw light upon the general nature of cerebellar control. These lower vestibular systems, vestibulo-spinal and vestibulo-mesencephalic, obviously can reach about all the voluntary musculatures. These paths are in the main simpler and more direct than the superior peduncular but there are, nevertheless, probably connections with the non-cerebellar extrapyramidal systems *via*, for example, the interstitial nucleus and the nucleus of the posterior commissure.

Speaking of the vestibulo-spinal tracts, who has ever used vestibular tests such as past-pointing, or pass-pointing, as an aid in diagnosing ventrolateral and ventral cord lesions? The vestibulo-spinal tracts lying in this region of the cord undoubtedly carry down the vestibular impulses which cause deviation in such tests and the deviations should be absent in cord lesions in the above location.

The general nature of the efferent paths of the lower vestibular circuits appears to be what one would expect in making the curious gyroscopic, plane-maintaining adjustments of limbs and eyes to translations of the whole animal through space but it is not improbable that the change in posture in man, as well as increased control by higher centers, may have thrown it out of gear or made it less important—except as a vertigo- and nausea-producing mechanism. Even these lower anatomic arrangements, however, have not been made entirely clear—much less the exact relation with and influence upon it of the superimposed cerebellar mechanism. It would be well then, if we knew clinically the exact difference between disturbances due to lesions and stimulation along the more direct vestibular routes and those seen in cerebellar lesions. Holmes has shown differences in nystagmic movements apparently. The view that the past-pointing reaction passes solely through the cerebellum is, I take it, not now so generally held as formerly, but there should, it seems, be some alteration of this reaction in lesions of the superimposed cerebellar circuit.

Turning to the other great outlet, the superior peduncle, we are

struck with the fact that we encounter first a linearly extended convoluted nucleus, the nucleus dentatus, and next a round massive nucleus, the nucleus ruber. The character of the former is due to the necessity of accommodating a great mass of cerebellar cortical fibers, from the cells of Purkinje, which end in it. This is also shown by its absence in forms with less developed cerebellar cortex. While there is still the possibility that some Purkinje axones emerge from the cerebellum without interruption, it does not seem probable that the number is considerable in the cerebellum of higher forms. It is the same necessity, in reverse, as that which produced the convoluted inferior olive, in the case of the dentate there being concentration instead of diffusion; and just as, when we go backward along the olive, we only encounter tracts of obscure origin so when we pass beyond the dentate we only encounter a massive nucleus and other rather obscure connections. In the case of the dentate there is probably also an areal correspondence with the cortex but how about the nucleus ruber, its most important connection in the other direction? Everything points to the latter as a great nodal point with many afferent and efferent connections both upwards and downwards and to its being used to carry the successively concentrated cerebellar influence in many directions, as well as to its being to some extent an important complex reflex center.

Incidentally, it may be remarked that the curious double-crossing of the dentato-rubro-spinal path is easily accounted for by the fact that the nucleus ruber is in connection, on the one hand, with higher centers exerting heterolateral body control and with the cerebellum which exerts an ipsolateral control.

Before discussing this further, it may be well to point out some defects—and crucial defects—in our knowledge of this region and especially of the nucleus ruber, even aside from the mystery involved in the fact that we encounter the extrapyramidal tangle.

One problem which arises is: Does the ruber receive paleocerebellar (*i.e.*, spino- and vestibulo-cerebellar) influences? It seems probable that the globose and emboliform nuclei represent such a connection but not perhaps established. Assuming this to be the fact, do these nuclei innervate the paleo-ruber the neo-ruber, or both? *A priori*, morphological considerations would favor the first view, but has it been established?

Again, is there a complete blending of efferent cerebellar influences

in such structures as the dentate and rubral nuclei? Previous consideration of the dorsal column nuclei would seem to show that this cannot be assumed with certainty; but we are now dealing with *descending* integrating systems and it is not for nothing that the pyramidal fibers, with their well marked topographical or segmental control, avoid interruptions in gray matter until they reach the level at which they act. If this "mixture" takes place the synthesis of the whole or of large portions of the cerebellar cortex are projected upon each of the peripheral motor mechanisms under cerebellar regulation, there being, however, considerable probability that the two outflows do differ physiologically from each other. Obviously a more minute analysis of the above structures, if possible, is necessary to give an anatomic answer to this question.

One of the first facts that attracts our attention is the apparently slight character of what seems to be the path of direct cerebellar control to the body by way of the superior peduncle. It is pretty well agreed that the only well known path is *via* the rubrospinal tract, also that this tract is comparatively small in man and that the cells from which it originates—the large paleorubral cells—are few in number. There are, perhaps, four explanations: one is that cells of the neo-ruber act as intercalated cells and the impulses passing along the increased number of peduncular fibers are thereby further concentrated upon the paleo-ruber. Even so, one would expect an increase in the old rubro-spinal tract to meet the increased load and such does not appear to be the case.

Another explanation is that there may be undiscovered descending tracts which perhaps have eluded observation because they are composed of fine, possibly amyelinated, fibers. Here it may be remarked that while the absence of myelin probably does not have in all cases the same significance, yet amyelinated fibers are of a lower grade of development and it is not improbable that they may also, naturally, in some cases represent more recent acquisitions of the nervous system. The pyramidal tract as seen in some other mammals is a case in point and the tract of Helweg may be another example. The discovery of other important descending rubral connections would simplify a comprehension of cerebellar activities.

A third explanation would emphasize the importance of those superior peduncular fibers which end in the reticular formation—aside from those to oculomotor nuclei—and also the rubro-reticular

connection observed by von Monakow. This would give a polysynaptic descending reticulo-spinal path. Apropos of this, it may be remarked that degenerations reveal a large number of spino-spinal fibers in the human cord and it may be that this complicated, diffuse, spinal mechanism, no longer so much an independent spinal reflex apparatus in man, may be played upon by descending reticulo-spinal and other descending extrapyramidal systems. This might account in part for the more diffuse character of many of the abnormal involuntary movements in man as contrasted with the more individualized pyramidal movements, though the hyperkinesia or "mass reflex" seen in certain cases of transverse cord lesions is not, of course, identical with the abnormal movements "released" by higher lesions. Both the reticulo-spinal and spino-spinal systems might receive more consideration but it seems doubtful if the reticular formation, after subtracting the known newer connections, such as neo-ruber and central segmental tract, imbedded in it, shows any greater development in man.

Still another explanation of the paucity of direct descending paths representing continuations of the efferent superior peduncular connection is that the newer path of the ruber represents connections with higher neöencephalic parts of the brain. Present evidence favors this view, *i.e.*, important connections with the pallium and neo-thalamus.

Regarding the nature of the pallial connections with the ruber, we appear to have the three possible views: that the connection is rubro-pallial, or pallio-rubral or both (von Monakow), with perhaps an increasing tendency to regard the connection as principally rubro-pallial. The neothalamic connections may also represent part of a rubro-pallial path or may be part of a rubro-thalamo-striatal path. This latter, coupled with the existence of pallido-rubral fibers would give a return circuit to the ruber and if we think this necessitates a descending path for the resulting integrations we are thrown back upon our inadequate rubro-spinal system. It must be remembered that the ruber probably has connections with the colliculi, which enable us to utilize the posterior or medial longitudinal and predorsal bundles. On the other hand, reciprocal connections between two masses of gray may have a general physiological function by modifying the intensity (reinforcing? inhibiting?) changing the timing or securing a more even diffusion by means of this back-lash. Such a general function would

seem to be more likely, perhaps, where the reciprocal relation is between two identical structures, which would be the case apparently with the rubro-pallial connections but not with the rubro-striatal. Reciprocal connections are apparently present in many parts of the nervous system.

Pursuing this matter further, if we accept the rubro-pallial character of much of the superior peduncular outflow, coupled with the existence of the pallio-ponto-cerebellar connection, we reach the rather surprising conclusion that the pallio-cerebellar connections as a whole in the main represent reciprocal influence. Moreover, if we consider the more direct cerebellar connections to lower centers as inadequate, we are driven to the conclusion that the main efferent path or paths for the projection of this vast reciprocal cerebello-pallial integration upon lower centers must be either by the pyramidal or the pallio-thalamic paths or both. If by the pallio-thalamic, we would probably ultimately impinge upon our rather inadequate but only imperfectly known lower extrapyramidal paths such as rubro-spinal and medial fasciculi. It will be noted, parenthetically, that the pallial areas connected with the ruber are probably not, in the main, the same as those originating the pallio-pontile fibers. If by the pyramidal path we reach the interesting conclusion that the pyramidal tract has in it an indirect cerebellar component. This would explain the impossibility of voluntarily suppressing a cerebellar dysmetria say—assuming such impossibility exists—the only remedy being to substitute a voluntary compensatory act calculated to reduce the disturbance, *e.g.*, the dysmetria slows up or stops before a certain desired point is reached. A careful study of volitional movements in cases of cerebellar ataxia might disprove, but not prove this view. They would not prove it because the pallial cerebellar components in normal voluntary movement if transmitted *via* the pallio-ponto-cerebello-rubro-spinal etc., path may be equally involuntary in character.

— If we revert to the view that the connection between ruber and pallium is pallio-rubral an additional load is placed upon the rubro-spinal.

This all shows the importance of a more definite knowledge regarding the size of this tract in man. Older investigators of the nervous system did considerable fiber counting and there have been sporadic renewals of this since then. Such investigations have more than an academic value as satisfying a fastidious demand for meticulous

accuracy. Knowledge of the number of fibers in various fiber systems is one of the foundation stones for a correct understanding of how the nervous system does its work.

When we pass beyond the fastigial and dentate nuclei we are no longer dealing purely with intracerebellar integrations but with integrations of cerebellar influences with extracerebellar ones. In all these successive integrations we must look to further advances in our general conceptions of interneuronal interaction combined with an even more accurate knowledge of finer histological relations. The great body of information placed in our hands by Cajal has not even now been fully utilized and must also be amplified in many directions, including verification of certain details, especially concerning collaterals, in adult human and anthropoid material. In addition to this, all of our Weigert myelin and degeneration myelin work must be repeated in axis cylinder pictures.

When we view the above efferent cerebellar connections and also the probable rubro-thalamo-striatal path we at least see that the anatomic mechanism is present for what we also see in clinical cases, *i.e.*, that the cerebellar regulative activity is exerted upon—or present in—all activities of voluntary muscles from reflexes to complicated voluntary activities, even in those concerned in such highly skilled acts involving non-posture maintaining muscles as speech. We also see that of the two great outflows, the one *via* the fastigium would apparently have more to do with the posture maintaining mechanisms of a vestibular and spinal character while the dentato-globoso-emboliform one would have more to do with all the forebrain reactions, both the learned voluntary ones and the more automatic, emotional and semi-voluntary ones which fill out the forebrain reactions, and which include postural adjustments as well as individual movements. This view, however, is based upon the assumption of no complete or very extensive overlap in the cerebellar areas drained by these two outlets. There is probably considerable overlap, at least in the drainage by the various internal cerebellar nuclei.

One question, referred to already by Walshe, is why the symptoms observed in cerebellar lesions—cerebellar ataxia—are not identical with those observed in lesions of the superior peduncle which, on the contrary, appear to be involuntary movements of a choreiform or choreo-athetoid character. It must be remembered that in the case of superior peduncular lesions—on which we need more observations

by the way—not all of the efferent cerebellar paths are cut; there still remains the fastigio-vestibular outlet.

If we had at our disposal careful comparisons of the disorders due to lesions of each of these—as well as of each of the afferent connections—whether they can be differentiated or not, light would be thrown upon the nature of the cerebellar control. Another point that arises in connection with the above discrepancy between the effects of cerebellar and superior peduncular lesions is what is the difference between the ataxic and the abnormal involuntary movements above alluded to? I take it that one at least of the important differences is that the latter are apparently more spontaneous. What this spontaneity probably really means is that the latter are more easily elicited by afferent tonic stimuli acting while the part affected is apparently in complete rest, actually is moving little or none but is incompletely supported, in other words a species of static ataxia. These movements also are elicited or increased by effort and by emotion, and attention often has an effect upon them—not always of the same character. That there is a cerebellar component in them follows from what has been said above.

On the other hand, if we take the disturbances due to rubral lesions in man in the cases cited by Rademaker, we find they are inability to assume or ataxia in assuming and maintaining an upright posture, tremor, hypertonia and occasionally choreiform or athetoid movements. In regard to the first two, at least, the picture closely corresponds to that seen in cerebellar lesions. In individual cases the correspondence is very close. In other words, we see what might be expected in view of the massive cerebello-rubral connection. The question of hypertonia will be mentioned later. There immediately arises, however, the questions raised by the apparently negative results (Magnus) of cerebellar extirpation upon the rubral righting reflex center. It seems to the writer that there is no real difficulty here. When the animal was decerebrated all pallial activities ceased. It has already been seen that the superior peduncle represents largely a continuation of the pallio-cerebellar path and consequently the cerebellar regulation of pallial activities. These activities are, broadly speaking, in man the result of vast multisensory mnemonic associations, probably represented largely by the “spontaneous” movements absent in the decerebrated experimental animals, and where they are absent their cerebellar regulation is also naturally

absent. On the other hand, cerebellar injuries in otherwise intact animals do result in disturbance of movement and posture maintenance. The above results, then, are partly confirmatory of the view that the neo-cerebellum is in general a mechanism regulating pallial activities. It is extremely interesting, if Rademaker's views as to the function of the ruber be correct, to see that there is provided a complex reflex center, upon which pallial activities can play in securing proper adjustments of the lower postural mechanisms during its activity. The increase of the ruber in man tends to confirm this view. How far there is a shift to the neo-ruber and what that shift consists in, is a further interesting question. One cannot admit that man can assume and maintain his normal upright posture without his cerebral hemispheres, whatever the tonus distribution may be in their absence. In fact, the rigidity observed in Edinger's case of a decerebrate child cannot be attributed to a rubral lesion if the only rubral change was a secondary degeneration on atrophy of its neöencephalic portion. This suprareflex regulative activity of the cerebellum is seen also by the experiments of Magnus and De Kleijn which show that the various body, neck and vestibular tonic reflexes are intact when the cerebellum is removed. Returning to the superior peduncle, it may be remarked that it is the most massive afferent connection of the ruber and that in cases of unilateral neo-cerebellar agenesis the opposite ruber is practically absent—the neo-ruber at least. In view of this, any experimental work interpreted as negative with respect to cerebello-rubral influence must be regarded as either inadequate as to method or erroneous as to interpretation. Here anatomy must take precedence over experiment, if there be a conflict between the two.

If we were strictly logical we would, then, to explain any discrepancy between the effects of cerebellar and superior peduncular lesions, in the first place minimize the differences between the two kinds of disturbance of movement and what differences there are we would attribute to the spino-vestibulo-cerebello-fastigio-vestibulo-spinal mechanism being affected in the cerebellar lesion but not in the superior peduncular one or not so much so. It is thinkable that the activity of this split off portion acting on lower centers, in part at least, accounts for the unequal tonic maintenance possibly underlying the disturbances seen in superior peduncular lesions. While the anatomists cannot give the anatomic side of many functional phenomena, it is also true that the physiologist might follow—and is now

following, by the way—more closely anatomic suggestions, rather than the simple transverse cut, for example, in his experimental work and the clinician likewise, often, in his observations. To take examples already known, the anatomist would not expect *a priori* to find sensory changes in cerebellar ataxia nor even in certain abnormal involuntary movements. Might not more be looked for using anatomic clues? Again, could not more be gained even without autopsy in all cases by carefully noting combinations and dissociations of clinical symptoms as Head did in his work on the central paths of sensation?

The discussion of extrapyramidal questions is to be avoided here for the double reason of their intricacy and difficulty and of the writer's ignorance, but it may be remarked that many postures are not maintained by gravity tensions. Probably nearly everyone present is holding the fingers partly flexed but not against gravity. Is this flexion due to greater strength of the finger flexors and they are "stronger" than the extensors, or is it due to some mechanical arrangement of ligaments and bones, or is it a real slight difference of tone between the two groups? That there is such a neural "holding" in certain postures, in the case of individual parts, possibly by spinal circuits, is shown by certain experiments. Just as we must conceive of our general bodily feeling of welfare or illfare to be due in part at least to a constant stream of affective stimuli from viscera and environment so must we conceive of posture as maintained, in considerable part at least, by a continuous stream of proprioceptive impulses from the organs of motion and holding, which stream splits after entering the central nervous system into many streams: to cord circuits, cerebellum, midbrain, basal ganglia and pallium. Probably all true ataxia and much hypotonia are due to cutting off one or more of these afferent streams to a given central structure or structures or inquiry to proprioceptive coördinating centers. It almost seems, on the other hand, that we could further generalize and say that abnormal involuntary movements and hypertonias are due to lesions more on the descending side. Lesion of proprioceptive mechanisms must always result in disturbances of tone and movement.

While much of tonus is thus maintained, we cannot perhaps in the broadest sense conceive of all tonus or posture, or perhaps we should say continuously maintained muscular tensions, as due solely to proprioceptive stimuli. While tonus probably cannot be properly

maintained pyramidally (*i.e.*, by continuous voluntary effort), extra-pyramidally, or reflexly without the assistance of proprioceptive stimuli, into the tensions maintained in emotional states, mostly unconsciously or involuntarily, there also enter stimuli from different sources, probably affective, especially visceral, and also endocrine. It may be that these latter influences are especially responsible for the tonic changes often attributed to basal ganglia lesions. This would be the component which would be most likely to have a peripheral sympathetic outflow if, as seems unlikely at present, a sympathetic tonic or kinetic influence upon voluntary musculatures should be established. We may, in fact, broadly look upon the organism as a whole in a state of continuously maintained, though changing, endocrine, visceral and proprioceptive equilibrium repeatedly upset by clonic reactions induced principally, but by no means entirely, by exteroceptive stimuli, *i.e.* by more abrupt changes in these various internal and external stimuli. The cortex pallii receives its more immediate activation mainly, perhaps, from the last but by it are blended the others as well.

In any case, the pallio-ponto-cerebellar connection, whether it be regarded as representing part of a reciprocal interaction between pallium and cerebellum with other pallial outlets as a final common path or whether it be regarded as an indirect outlet for pallial influences via rubro-spinal and other tegmental paths, it is evident that the cerebellum receives impulses which are at the most only indirectly proprioceptive. We may conceive of the pyramid to be set in activity by a synthesis of some sensory impulse, say exteroceptive (the immediate stimulus) linked mnemonically with a similar past stimulus ("gnosis"), with various past and present visceral and other protopathic impulses (the emotional, wish element), with past proprioceptive stimuli (skill or "praxis" and "conation"), and guided in its execution by concurrent proprioceptive stimuli. Accompanying this is a setting into activity of all the non-cerebellar supplementary extrapyramidal machinery, with its tonic, sthenic and expressional contributions, and of the cerebellar mechanism with its regulation of the execution of both of the above, if we accept the more usual view of a separate cerebellar outlet to the lower motor centers for the accessory pallio-cerebellar component. If we regard the pyramid as the principal final outlet, the question (usually ignored) of the existence in adult man of pyramidal collaterals to basal ganglia and

pontile nuclei, as well as to reticular formation, observed by Cajal, assumes even greater importance. Whichever view we take, the pallio-cerebellar path would carry to the cerebellum pallial syntheses into which not improbably other than proprioceptive elements enter and at the most such proprioceptive influence would only reach the cerebellum by a most circuitous route. In any case, the interesting fact emerges that all activities of voluntary musculatures must receive impulses that pass through the cerebellar cortex. If we regard the more primitive paleocerebellum in lower forms as coördinating proprioceptive stimuli and then handing them on to the lower motor and also more primitive forebrain motor centers, it is evident that more complicated relations come in with the pallium, where the cerebellum cannot be regarded as simply acting directly upon motor mechanisms, whether there be important cerebello-pallial connections or not. Perhaps further investigations of cephalad cerebellar connections in lower forms might throw more light upon the nature of this mechanism.

Regarding the hyperactivity of certain reactions when "released" by interruption of connection with some other perhaps "higher" center, the writer sympathizes with Dr. Pike's conception of this phenomenon, in line with Hughling Jackson's view, as due more to an increase of impulses acting through the lower circuit than a loss of some constant inhibitory influence exerted by the higher center upon the latter. Stimuli which normally pass in part down through the pyramidal tract are, in lesions of this tract, diverted, so to speak, through the lower spastic-producing reflex circuit, on the basis of the ordinary view that the spasticity in question is due to a lesion of pallio-spinal fibers. It is true we must think of the pyramidal influence in normal conditions as prevailing over other, tonus-maintaining, mechanisms, such *must* be the case for the pyramid to function, but the above view emphasizes less some rather mystical continuous restraining pyramidal influence and more a more intelligible active stimulation. Regarding the question, raised by some, as to whether the spasticity usually attributed to pyramidal lesion is really due in part or whole to a lesions of this tract, attention might be called to the importance of careful clinical observation of cases of inferior (hypoglossal) alternating hemiplegia, especially when unaccompanied by an disturbance of the sense of position and movement. In cases of this kind we have a pure pyramidal lesion without any involvement of extrapyramidal, afferent cerebellar or afferent

pallial systems which might enter into questions of tonus, unless such fibers are present at this level in the pyramid itself. The writer has always supposed that there is no especial difference between the pyramidal signs in a lesion here than in lesions involving it at other levels.

The fact that the pallio-cerebellar path is open in cases of pyramidal lesions would seem to lead to the conclusion that the spasticity usually attributed to its lesions might be due, in part, to an overaction of the pallio-cerebellar system, if we accept the view that the latter has a separate lower outlet, due to an increase of pallial cortical impulses acting upon it in the absence of the pyramidal outlet—or, if you will, to an absence of an inhibiting influence normally exercised over it by the motor cortical areas. The spasticity and posture in pyramidal lesions does not appear to be what would arise from released, low segmental tonic circuits but here again, the neglected pyramidal collaterals must be taken into account. The mechanism of voluntary relaxation—which may be different from that of voluntary movement—should also be studied. Another possible explanation of the spasticity in question, if due to pyramidal lesion, which should be taken more seriously into consideration, is that it is due to an over-activity of pallio-thalamic or pallio-rubral systems. The former, however, would more probably produce disturbances more of a choreo-athetoid character, which resemble distorted emotional expressions. The latter, the pallio-rubral, should obviously demand more serious consideration.

From the preceding discussion one possible view of cerebellar activity which emerges would view the cerebellum as a nodal point in which all its afferent impulses are mixed in a common pool and then distributed to various points where they are successively integrated with other impulses until the final common path is reached. A partial view of this kind would concede a certain amount of "somatotopic" localization and a certain amount of difference between the activities of the paleo- and neocerebellum.

Would such a mechanism require a cortex? Would not a large lump nucleus with shorter axone neurones intercalated be adequate? The fact that we have an elaborate cortex suggests a more complicated function.

It is strange that with our accurate knowledge of the cerebellar cortex we cannot interpret it better, but from what precedes it is

obvious that a great part of this difficulty arises from defects in our knowledge of the afferent and efferent cerebellar connections and their exact representation in the cerebellar cortex, as well as our ignorance of the general meaning of the various finer interneuronal connections.

The cerebellar cortex differs from the pallial in that it probably receives solely or mainly one kind of stimulus, direct protopathic and exteroceptive impulses being probably absent, and that there is no definite evidence of great mnemonic capacity. If this latter statement be true, it, coupled with the late development of the cerebellum, would appear to show that the mnemonic activity of the pallial cortex does not rest upon its late ontogenetic development—its immaturity at and after birth. Even here, however, it is thinkable, but not at all probable, that the skilled acts and also the various habits of posture and activity which make up the external manifestations of personality and which are probably represented by certain acquired arrangements of the inherited pallial cortex, may be linked with analogous acquired or mnemonic changes in the cerebellar cortex.

These two differences—absence of variety of stimuli and absence of memory—would partly account for the uniform character of the cerebellar cortex and the probable absence of long association connections between different cortical areas. Impulses entering are spread out over a certain area, “corticated,” and sent out. The association mechanism would appear to be provided more in the successive spreads through afferent nuclei and their common diffusion, such as the olivary, pontile, and partly segmental spinal nuclei, upon the cortex and the successive integrations by the nuclei in the efferent paths.

As far as the cortex is concerned, it appears to do the same thing to all its afferent impulses whether they come from pallium or more directly from receptors.

In the interpretation of the cerebellum and of the cerebellar cortex we are met at the outset by a barrier, *i.e.*, our lack of knowledge of the respective origins of the climbing and mossy fibers. Most of the discussions of this question have been based upon the assumption that these fibers have different origins. The writer would like to question this assumption and advance the counter one that all masses of gray sending fibers to the cerebellar cortex send both kinds of fibers. A third alternative is the one rather recently advocated by Lorente de Nó, *i.e.*, that the climbing fibers arise from the cerebellar cortex

itself, probably from the cells of Purkinje, such cells forming a separate category. Some of the cells of Purkinje would thus be cortical association neurones. Such a view opens up a new and interesting vista. It is difficult to see, however, how such cells can be different from the others as far as reception goes. There seems to be every evidence that all Purkinje cells are in connection with granule cell and basket cell axones. It is possible, though, that only certain cells receive climbing fibers. This only emphasizes the need, pointed out elsewhere, for a thorough areal study of the cerebellar cortex, using all methods. These important questions can be determined by an intensive study of cerebellar cortical areas which receive fibers from one or another source although this would perhaps only, at the most, differentiate paleo- from neo-cortical areas. There have, however, as far as I know, no such areal differences been definitely made out. In fact, one striking thing about the cerebellar cortex is its apparent uniformity in all parts and in all animals where present, though exhibiting a progressive development in higher mammals. Nevertheless, a careful study of the cerebellar cortex should be made. Another method would be a study of *axonal* secondary degeneration, using silver stains, after cutting various afferent cerebellar connections.

When we view the process of "cortication" we find we have the following: a possible direct return or shorter cortical circuit provided by the climbing fibers and a longer one provided by mossy fibers, granule cells and basket cells and involving a spread both lengthwise and transversely along the laminae. Also a short spread by collaterals of Purkinje cell axones. There also appears to be a reciprocal or back-lash circuit involving granule and van Gehuchten cells. Analogies to this arrangement may be seen in the dorsal gray horn, the gelatinosa corresponding to the granule layer, as pointed out, I think, by Johnston years ago; also perhaps more remote analogies in the pallial cortex and elsewhere.

Attention might be called especially to the spread by Purkinje collaterals. Axone collaterals originating near the cell body are of nearly universal occurrence in the central nervous system, suggesting, perhaps, some universal function. It is obvious that a blocking of the impulses passing along the axone by say a synaptic change in a refractory period might cause a collateral overflow into adjacent neurones of similar connections, but whether this would mean a compensatory "evening" of the impulses, or some reciprocal innervation, it is difficult

to tell. In this and in the overlap of afferent diffusions, previously mentioned, may lie, in part, the mechanism for the restoration of function after various lesions. "Centers" in cortices may be simply *predominating* areas for certain receptions or emissions with possibility of spread by the overlaps to other such centers, provided the lesion be not too extensive.

Whether the cerebellar cortex is simply doing on a vaster scale to all impulses of a certain character and in a more precise way what is done elsewhere in various parts of the gray matter of the central nervous system or whether there is something peculiar to the requirements of cerebellar regulation is difficult to tell but it is obvious that here as elsewhere we are witnessing, and will witness, a rapprochement between the neurologist with his rather crude explanations made to fit clinical observations and the general neuro-physiologist with his all-or-none principle, his refractory periods, summations, facilitations, inhibitions, etc., but with incomplete knowledge of clinical problems and sometimes of neuro-anatomy.

Returning to the question, why a cerebellar cortex at all? we might glance at one or two theories of cerebellar activity.

While it is said that there is a trend against the tonic theory of cerebellar function there is much in it which appeals to the writer, following lines of thought expressed by Walshe some time ago—in seeking the explanation of various phenomena seen in cerebellar lesions as fundamentally due to diminished tone—although possibly modified along lines of thought expressed by Mills, Weisenburg, Hunt, Tilney and Pike.

In general in discussing the function of any coördinating mechanism there are two questions to be discussed: a topographic or somatotopic one—the coördination of spatially separate parts; and a qualitative one—the change in the state of each part. In cerebellar disorders we see a difficulty in maintaining postures requiring complicated and delicate readjustments—in which I would include standing and maintaining equilibrium during walking and various acts—in maintaining postures necessary for the performance of certain movements and acts—fixations, and in the even performance of movement itself—steadiness and eumetria (the motofacient component of Tilney).

In all these there are two elements: one is not exactly perhaps the maintenance of an even tone but also the continuous adjustment of tone in maintaining positions of unstable equilibrium and during the

performance of movement in the moving part itself. The other, the topographic element, is seen in the proper localization of these tonic adjustments in the parts requiring them in the various activities indicated above. It is the latter in the various muscles involved that is expressed in the concept of synergy. The synergy can, however, consist only in the proper amount of simultaneous tonic or kinetic activity or both in the performance of some movement or movements. The change or adjustment of tone during an isolated movement, in the moving part, would perhaps involve only the antagonist muscle or muscles, though not necessarily so. A working conception on the basis of increase of both might be easier from an anatomical point of view as not requiring so complicated a mechanism, as well as explaining cerebellar asthenia. The presence of this tonic component during movement is seen in the difference between the movements of an atonic tabetic and a hypertonic Parkinsonian. The difference between motion in atonic and tonic conditions is much like that between the motions of flail-jointed dolls and those with friction joints. The parts of the latter stay in positions in which they are put and passive movement is different. A closer analogy would be where the tonus of the various muscles is represented by rubber bands which do not during passive (*i.e.* imposed from without) movement, either stretch or relax. The question is complicated by the combinations with active shortening of some of the muscles to extracerebellar influences, but the point is that the cerebellar flow into the muscles is equal for all. The same might apply to the more static mechanisms, as standing and fixation. This would enable us to construct a tentative anatomico-physiological theory which postulates an *even* diffusion by the cerebellar cortex of tonic impulses spread over appropriate cortical areas by the general but not necessarily universal diffusions of afferent fibers from the various subcerebellar nuclei—whether conveying direct proprioceptive stimuli or stimuli from more indirect sources. The topographic element is determined by the distribution of the afferent fibers upon the cortex, the equalization of the tonic modification by intracortical processes which seem well adapted in a general way to secure this result. Or we may take the view that the cerebellar influence is to equalize the tonus of the lower reflex mechanisms. This would require a varying intensity of the cerebellar influence. Lorente de Nó has well said that the cerebellum does not so much perform reflexes as exalt the activity of some and depress the

activity of others. This view might require a variable outflow which would not necessarily result in an equalization of tonus. In any case, cerebellar activity might be roughly compared to the governor of an engine with its automatic continuously acting plus-and-minus influence, thereby maintaining, so to speak, a constant tonic pressure. Allusion has already been made to the discrepancy between rubral lesions which appear to cause hypertonicity and cerebellar lesions which appear more usually to result in hypotonicity. This has been accounted for by others by assuming that the cerebellum has an inhibiting influence upon the ruber. According to the above view the cerebellar influence might be either to increase or decrease tone in various circumstances and also do both simultaneously in an areal way. In this, as in the purely inhibiting view, we encounter the inhibition mystery, but if the pallial cortex can simultaneously "voluntarily" shorten some muscles and relax others (*e.g.*, "letting" an elevated arm fall) why cannot the cerebellar cortex "involuntarily" and areally raise tonus in some parts and decrease it in others? It is obvious that if we attribute to the cerebellar cortex such a plastic adjusting activity, the variability, ambiguity, and contradictions seen in the results of various experiments and also in clinical cases may be thereby explained and it is also obvious that for such a complex function as involved in any one of the above views, a cortex is necessary. If, however, we have to choose between a uniform increase and a uniform diminution of tone as an expression of cerebellar activity it would be the former which would be chosen, for certainly cerebellar disturbances admit best of explanation by a general hypotonia as shown in the article by Walshe already alluded to. It may be objected that the "tonic" change of a moving part is practically a clonic change. I am not sure whether if this be true that it constitutes any more than a nominal objection unless it would seem to postulate a motor character to the cerebellum which experiment would seem to show it does not possess. When it is considered how this more abrupt change is, so to speak, secondarily linked with movement, this objection might not hold. It has never been entirely clear to the writer just why only those points of the pallial cortex in most direct connection with lower motor neurones yield motor reactions. Stimulation of other points of course would pass through more synapses to reach such direct connections, but it does not seem entirely clear why this should make the difference although this may be the explanation. It

may be that better stimulation methods may be found which will advance this method of research.

If the view of Lorente de Nó regarding association Purkinje cells be true and they provide a linkage of rather distant cortical areas, topographic coordination might be regarded as furnished by them instead, or partly instead, of the subcortical diffusion, or such connections might simply distribute the already integrated cortical adjustments of one area to another.

In any case, as previously remarked, the pallial cortex with its qualitatively different areas both on the receptive and emissive side and its complicated association mechanism appears to be quite different fundamentally in its arrangements from the cerebellar cortex. In the latter we have afferent diffusions probably all essentially alike qualitatively and only differing topographically. After "cortication" by the area to which they diffuse they pass out in successive concentrations and split into paths to the various infracerebellar motor systems, and perhaps the supracerebellar pallium, whose activities they regulate.

One point which should be considered in relation to cerebellar activity is the question of what might be called peripheral repercussion. The activities of various reciprocal innervations obtaining between various parts of the central nervous system might be termed central repercussion. By peripheral repercussion we mean the explanation of a central function by peripheral stimuli set in activity by the central nervous system and returning to the activating center.

Undoubtedly in all activities but especially in proprioceptive ones there is a continuous, so to speak, alternating back and forth flow of impulses from, to and from periphery to center. As each new posture is assumed a fresh set of proprioceptive stimuli stream in and lead to further adjustments. What is meant here, however, are more extreme theories. The James-Lange theory of emotion which identifies emotion with visceral and perhaps other "sensations" aroused by mnemonic cortical conditioned reflex activity is one. Another is the Watson theory of identification, as I understand it, of various "mental" operations with the cortical reception of proprioceptive impulses from various muscles, especially of speech, set in activity by cortical mechanisms. Undoubtedly the visceral or proprioceptive reverberation may play an important part in emotion or in mental activity, respectively, and, in the latter case, certainly in the acquisition of

skilled movements, but the extreme forms of such theories appear to attempt to minimize unduly or even do away with the importance of the pallial associative mnemonic mechanisms. Similar questions arise in connection with the explanation of the reinforcement of the deep reflexes and of various abnormal associated and involuntary movements by muscular effort of some other part, also by emotion. Into this question there enters the question, mentioned earlier, as to the independent activity of lower reflex circuits. It is easy to see, for example, how an increased action exerted by a higher center upon such a lower circuit, if summated with other afferent impulses received by such a lower center would cause a change in the muscles which would in turn start a new reflex activity through the lower circuit. A re-percussion theory in the case of the cerebellum would be that the cerebellar adjustments take place *after* the reception by it of a peripheral proprioceptive stimulus, initiated by impulses from some other part of the central nervous system. Of course any new adjustment—change of posture and movement—arises from a bed, or basis, or foundation of an existing proprioceptive equilibrium maintained by proprioceptive stimuli, but the pallio-cerebellar connections render it possible to imagine that—in the case of say a voluntary movement—it need not wait until the movement is initiated and it receives the proprioceptive stimuli resulting therefrom but that its activity is initiated by the pallium concurrently with the pyramidal movement. Further work upon reaction times might be useful here. It is also evident, from what has been said, that unless there be found a more ample spread upon the cerebellar hemispheres of direct proprioceptive stimuli from the body, especially extremities, we must imagine the proprioceptive control of part at least of the neocerebellum reaches it only *via* the pallium. It might be worth while here to deepen our clinical observations by paying still more attention to whether the cerebellar disturbance, for example, affects more standing and walking or more individual voluntary movements—in passing how many look for the ataxic tongue—also whether there is any distinction between the voluntary skilled movements and the involuntary emotional ones. Is it or is it not true that cerebellar ataxia is increased by emotional states and by simultaneous voluntary effort exerted on other parts as is the case with the so-called abnormal involuntary movements, and how is it affected by attention?

Edinger long ago pointed out that cerebellar development in various

vertebrates varies with their complication of delicate adjustments in moving through space. An application of this to man would emphasize especially the requirements of his upright posture. The fact, however, that cerebellar disturbances manifest themselves equally in various voluntary activities not involving general bodily posture would seem to show that the emphasis is more upon the *finer* regulation and coördination of all movements and postural adjustments and that it is the development of the various mnemonic or neokinetic activities rather than only those involved in the upright posture itself, the latter correlated with the above to be sure, which has necessitated, so to speak, the great development of the cerebellum in man.

In brief, we find that we do not know the source and nature of many of the impulses projected upon the cerebellum by its various afferent paths nor the way in which such are affected in their passage through subcerebellar synapses; we do not know accurately in certain important details the areal projection of these various afferent paths upon the cerebellar cortex; there are still important critical details of cerebellar cortical structure, the ignorance of which also prevents our forming a conception of its activity—an added obstacle being our inadequate knowledge of general neuro-physiology and its formulation in structural terms; we do not know many important details as to the distribution of the cerebellar outflow. Consequently, we do not know how far there is a topographic representation, how far there is a blending or non-blending of different *forms* and combinations of activity such as postural and kinetic, older and newer, voluntary and involuntary and emotional. Nor do we know how far the organ functions more as a directly reacting or indirectly reacting mechanism.

It is also evident that we probably know less about neocerebellar than paleocerebellar connections.

CHAPTER II

THE MAMMALIAN CEREBELLUM

A COMPARATIVE STUDY OF THE ARBOR VITAE AND FOLIAL PATTERN

HENRY ALSOP RILEY, M.D.

THIS study represents a survey of the class of the mammalia from the point of view of the form of the arbor vitae and the folial pattern of the cerebellum. On account of certain deficiencies in the study collection, it is not yet complete. A number of the orders, such as the monotremes and the insectivores, are unrepresented by examples, and this is increasingly true in connection with many of the suborders, families, subfamilies and species which make up the class of the mammalia. As these forms become available they will be studied and will form the substance of a further communication on this subject.

In order that definite conclusions may be reached in regard to functional localization within the cerebellum on the basis of the characteristics of the folial pattern as compared with the physical organization of the animal providing the pattern, a much greater number of cerebella must be examined, not only to afford representatives of all of the orders, suborders, families and species which can be obtained, but also to provide a study of a number of individuals of each group, in order to determine whether the given folial pattern is common to all members of each species, or whether some of the variations which appear may not be individual divergences from a generally accepted pattern.

It should be a matter of considerable probability that the patterns evidenced in the disposition of the folial chain should have some direct relationship to the physical characteristics of the animal to which the particular cerebellum belongs. Therefore, in this study and in the continuation of it which will follow, the attempt has been made to collect diversified forms in order to determine whether there may be some deductions which can be drawn from the similarities or dissimilarities in the corporeal equipment of the animals and the form and pattern of the cerebellum possessed by each individual example.

The collection from which this material was obtained constitutes the comparative anatomic collection of the Department of Neurology of the College of Physicians and Surgeons, Medical Department of Columbia University. The collection was originated and presented to the neurological department by George S. Huntington, the late professor of anatomy, who received the major part of the material from the New York Zoological Garden, through the courtesy of the directors of the American Museum of Natural History.

At the last meeting of the Association for Research in Nervous and Mental Disease, the subject of the cerebellum was discussed, and at that time a small portion of this still incomplete study was presented. The researches of Elliot Smith, Bradley, Bolk, Ingvar, Kappers and Edinger provide the background on which this approach to a limited problem in connection with that baffling organ, the cerebellum, has been made.

SCHEMATIZATION AND DIVISION OF CEREBELLUM

The direct focus of the study was established through the diagrams of Bolk and his observations that the arrangement of the laminae in the cerebellum represent a continuous chain, beginning at that part of the vermis which forms the cephalic wall of the ventricular fastigium, the margo mesencephalicus, and extending backward through many twists and turns in an uninterrupted series of lamellae to the final termination of the folial pattern, the last folium of the nodulus which forms the caudal wall of the ventricular fastigium, the margo myelencephalicus.

In following this folial chain, the method which alone can make possible any clear comprehension of the pattern of the cerebellum is that which has been used by all those who have studied this phase of the cerebellum, that is, the reduction of the entire cerebellum to one plane. In the preparation of my diagrams, I have not followed this scheme with rigid exactitude on account of the fact that the drawing and presentation of the structures forming the under portion of the cerebellum, chiefly the *formatio vermicularis*, and the convoluted twistings of its cephalic extremity forming the *parafloccular* and *petrosal* region, is difficult to schematize in its true anatomic relationships. Therefore, the patterns presented are more or less a compromise between a complete unfolding and, as it were, a spreading out of the under surface, maintaining somewhat the relationship of the upper and lower portions.

Cerebellar schemas

In connection with the various schemas which have already been formulated, all of them present certain advantages and disadvantages. The one which seems to me to follow most clearly the anatomic organization of the cerebellum in which all of the members of the mammalian

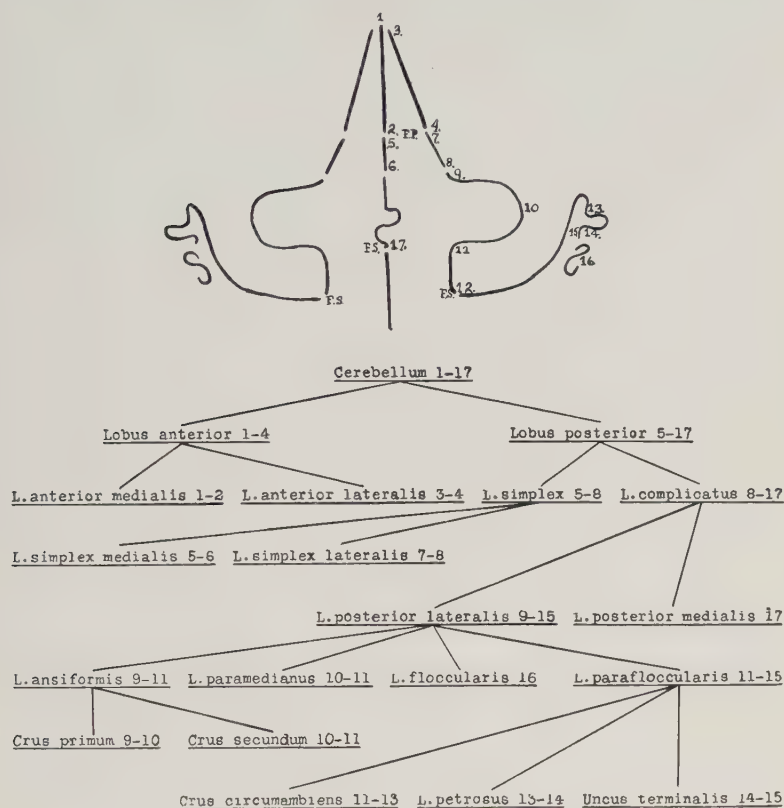


FIG. 1. The folial chain and its subdivisions

family are considered is that which was established by Bolk. I have, however, somewhat modified this schema (fig. 1). Bolk schematized his conception of the anterior lobe as an entirely undifferentiated structure not divided into a central vermal portion with lateral expansions forming a distinct lateral hemisphere. The studies of Edinger in his conceptions of a neocerebellum and paleocerebellum, of Brouwer

and his pupils, Oliver S. Strong and others in their descriptions of hemocerebellar atrophy, and of Langelaan in his embryologic identification of separate growth centers in the median and lateral portions of the anterior lobe, all make it quite certain that similar processes have been at work in the development of the anterior and posterior lobes and that each subdivision represents a central, vermal portion and a later hemispherical component. In connection with the anterior lobe, there cannot be any question that in certain forms even the lingula,

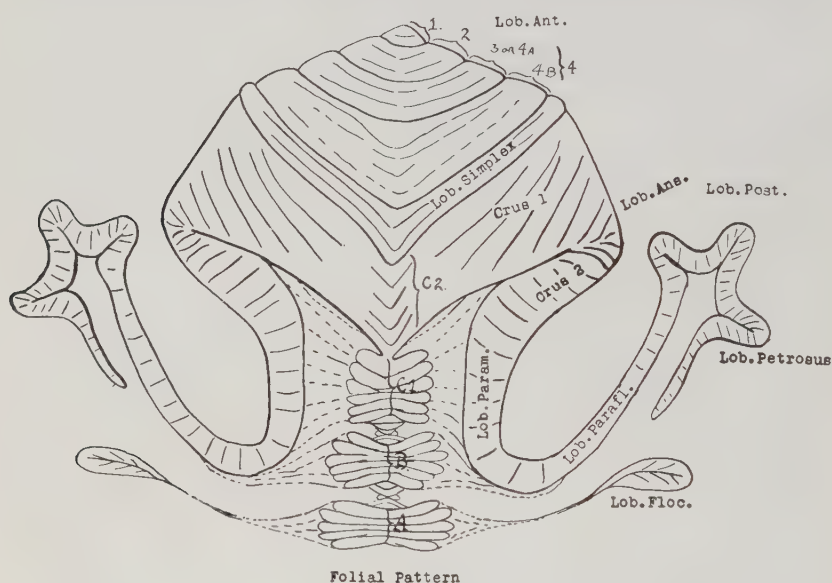


FIG. 2. A schematic representation of the folial pattern of the cerebellum, laid out in one plane.

lobulus 1, participates in the formation of the lateral extension, although this has been denied by Kappers. A consideration of the anterior lobe in *Cetacea* indicates an absolutely definite and distinct paravermian sulcus, more definite and deeper even than that which is found in the posterior lobe, a sulcus so deep that the foliation can only with difficulty be followed from the vermal into the lateral portion with absolute certainty and definition. In practically all of the other forms studied, an indication of a vermis can be made out, not only from the elevated form of the median portion of the anterior lobe but also

through the presence of short vermal sulci which can be seen extending outward for variable distances from the midline into the lateral extensions of the anterior lobe. In the modified schema of Bolk, I have, therefore, introduced lines representing distinct anterior lobe hemispherical constituents in the folial chain, in harmony with the arrangement universally accepted for the posterior lobe. This change has, of

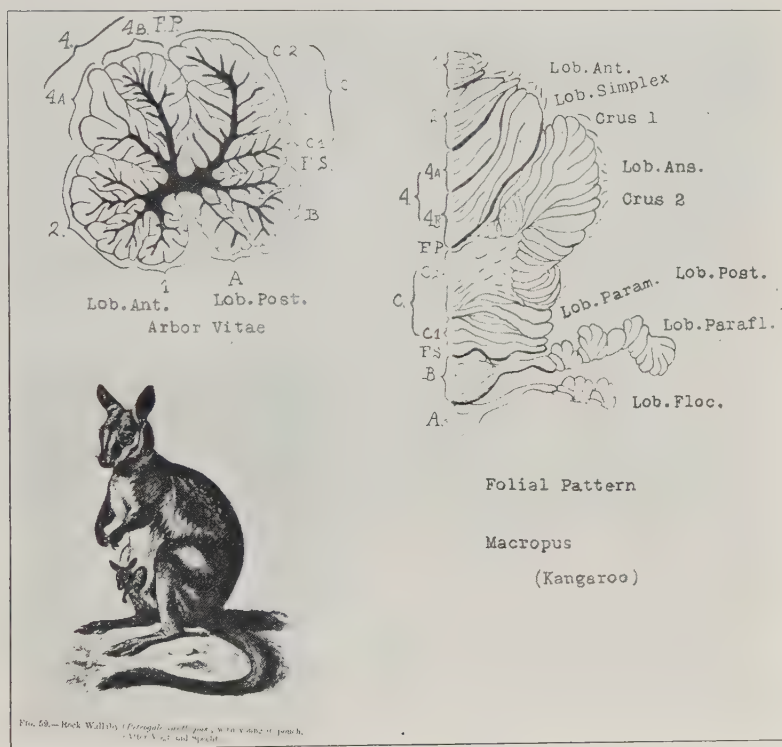


FIG. 3. *Macropus* (kangaroo)

necessity, materially altered the numbering which Bolk used in the determination of the various parts of the folial chain, and the modified diagram of Bolk has been renumbered to make evident the various portions of the folial chain by means of numerals indicating each individual part. No useful purpose can be attained by any material change in his nomenclature, and his divisions of the cerebellum seem

entirely satisfactory. The only deviation from this nomenclature is the substitution of the word *circumambiens* for the term *circumcludens* which Bolk used in connection with that part of the *formatio vermicularis* which lies in close proximity with the *lobulus ansiformis* and the *lobulus paramedianus*. The term *circumambiens* is familiar in anatomic nomenclature, and its general connotation is more easily recognized.

In figure 2, an attempt has been made to schematize the cerebellum as it has been studied, that is, as if it were spread out in a single plane. This diagram is somewhat more similar morphologically to the various anatomic divisions as found in the subanthropoid representations which have been studied than the schemas advanced by Bradley, Bolk, Elliot Smith and others. It, of course, does not bear any resemblance to the higher primates, since in them cerebellar organization has advanced to such an extent as almost completely to transform the basic features of the cerebellum. The schema also cannot faithfully reproduce the divergent specializations shown in the cerebella of *Bradypus*, *Pinnipedia*, *Proboscidea* or *Cetacea*. The schema also indicates the connections between the various subdivision of the vermal and lateral chain in the *lobus complicatus*.

The following list is an enumeration of the forms which have been studied thus far in this particular investigation:

- Eutheria
 - Marsupialia
 - Diprotodontia
 - Macropus
 - Polyprotodontia
 - Thylacinus cynocephalus
 - Edentata
 - Xenarthra
 - Myrmecohaga jubata
 - Bradypus tridactylus
 - Ungulata
 - Proboscidea
 - Elephas asiaticus
 - Artiodactyla
 - Camelus bactrianus
 - Rangifer tarandus
 - Giraffa camelopardalis
 - Bos
 - Sirenia
 - Manatus

- Cetacea
 - Delphinidae
 - Monodon monoceros*
 - Phocaena communis*
- Carnivora
 - Fissipedia
 - Felis domestica*
 - Canis familiaris*
 - Vulpes fulvus*
 - Cercoleptes caudivolvulus*
 - Nasua rufa*
 - Ursus americanus*
 - Pinnipedia
 - Otaria gillespii*
 - Odobaeus walrus*
 - Phoca vitulina*
- Rodentia
 - Simplicidentata
 - Castor canadensis*
 - Rattus norvegicus albinus*
 - Cavia porcellus*
 - Dasyprocta agouti*
 - Duplicidentata
 - Lepus cuniculus*
- Chiroptera
 - Megachiroptera
 - Pteropus
- Primates
 - Lemuroidea
 - Lemur varius*
 - Anthropoidea
 - Platyrrhina
 - Hapale jacchus*
 - Cebus lunatus*
 - Ateles ater*
 - Catarrhina
 - Macacus rhesus*
 - Cynocephalus babuin*
 - Simia satyrus*
 - Gorilla gorilla*
 - Anthropopithecus troglodytes*
 - Homo sapiens*

There are a number of elements which introduce a degree of uncertainty into any presentation of the pattern of the arbor vitae and the arrangement of the folial chain. In connection with the arbor vitae

the exactness of the median section makes a considerable difference, for a deviation from an almost exact sagittal section will produce a deformation of the arbor vitae which will materially alter the origin of the various medullary rays and, therefore, influence the lobulation which is dependent on the divisions of the medullary substance. The age of the animal also seems to exert, at least in some forms, a definite influence in the arrangement of the folial pattern. In the dog, for instance, one specimen in the collection, small and apparently from an immature animal, presented a perfectly straight vermis in connection with lobuli C 2 and C 1, whereas a cerebellum known to have been obtained from an adult animal showed a definite sigmoid gyrus in this portion of the vermal pattern.

The division of the cerebellum

The two chief landmarks in the study of the arbor vitae appear to be the fissura primaria and the ventricular fastigium. The other important landmark in the arbor vitae is the fissura secunda. In almost all of the forms examined, it was relatively easy to determine the position of the fissura primaria by its relationship to the ventricular fastigium, the fissure which penetrated the deepest, approached most closely to the ventricular fastigium and was the most vertical of the fissures of the arbor vitae being accepted as the fissura primaria. The fissura primaria and the ventricular fastigium divide the cerebellum into an anterior and a posterior lobe. The only order which presented any considerable problem in this differentiation was the cetacean in which great difficulty was experienced in determining the fissura primaria, and only a tentative decision could be reached through a study not only of the arbor vitae but also of the arrangement of the lobules in the folial pattern. Whether the assumption arrived at in the description of the arbor vitae and the folial pattern in the cetacean subdivision was the correct one is a question, but the decision was the best that could be reached under the circumstances. The fissura secunda was assumed to be the cleft separating lobulus B and lobulus C. This differentiation was in almost all cases a simple one to make. The continuation of this fissure laterally almost invariably led to the angle between the lobulus paramedianus and the lobulus parafloccularis, thus conforming with the embryologic differentiation in which the association of the vermal and lateral portions shows lobulus C 1 to be associated with the lobulus paramedianus and lobulus B with

the paraflocculus. This relationship is definitely settled in a considerable number of forms in which the connection between the lateral and the vermal folia is clearly visible, in many cases surface folia of lobulus C 1, and in other cases a submerged folium representing C 1, being found to be directly continuous with the most caudal folia of the lobulus paramedianus. No useful purpose seems to be gained by dividing the cerebellum into a middle and a posterior lobe through the location of the fissura secunda.

The division of the arbor vitae, following on the identification of the fissura primaria, the fissura secunda and the ventricular fastigium is, in general, a fairly simple matter, although in some details it presents conditions which may be susceptible of one or another interpretation. These differences of interpretation, however, are, in the great majority of cases, simply matters of detail and do not affect any of the essential characters of the division of the cerebellum into its constituent parts. The chief region in which these differences of interpretation may arise is in the origin of the second and fourth branches. The first branch is usually fairly clear, although it may be extremely rudimentary, of considerable size or form a lingula. The rays forming lobulus 2 arise singly or as a series of branches from the cephalic protrusion of the medullary substance. These may be fairly discrete, or a branch may be present which, arising from the dorsal and more caudal portion of the cephalic protrusion, may introduce the question as to whether the ray should be interpreted as an independent ray 3, or be grouped with either ray 2 or ray 4. The exact point of origin of the feet of these rays from the medullary substance may be changed by a slight deviation from an exact median section of the arbor vitae, and this may throw a portion of lobulus 2 into a distinct lobulus 3, or shift a distinct lobulus 3 into lobulus 4. The arrangement, however, of the folia forming the lateral outgrowth from lobuli 2, 3 and 4, is so simple and, in general, so uniform, that it is doubtful whether any definitely distinct function can be allocated to these portions of the cerebellum, which would be influenced by one group of folia belonging to lobulus 2, forming an independent lobulus 3 or belonging to lobulus 4. The arrangement of these lobules is, in general, so uniform throughout the entire series of cerebella which have been examined, that it is in all probability true that these lobuli serve portions of the body structure which are relatively uniform throughout the entire series, and do not present any material change in one form as compared with another.

The other branching of the arbor vitae in which there may be some difference of opinion is the exact determination of the point at which ray C takes its origin and its division into ray C 1 and ray C 2. Since, however, these lobules form a subdivision of a larger lobulus which shows, in general, a considerable degree of homogeneity throughout the entire series, here again the exact allocation of two or three folia to either one or the other lobule cannot be of great significance. The major variations in lobuli 2 and 4 are associated chiefly with the size and number of the rays acting as a scaffolding for the respective lobuli, and this, in general, seems to be more or less dependent on the corporeal bulk of the individual animal. Whether functional variations may also emerge on further study is a question only the future can answer. Continued investigation may disclose closer anatomic and functional relationships than are at present available. If this is the case, the variations in the anatomic arrangement of this portion of the cerebellum may assume a significance which they do not now possess.

So far as the connection between lobulus B and the paraflocculus and lobulus A and the flocculus is concerned, in some forms a definite bridgelike connection can be determined connecting lobulus B and the paraflocculus. When a direct connection is lacking, the general trend of the peduncle in the center of the folial roset of lobulus B is definitely turned in the direction of the angle of transition between the lobulus paramedianus and the lobulus parafloccularis. The connection between lobulus A and the lobulus floccularis is never so distinct. The line of the peduncle is clearly ventral to that taken by the peduncle of lobulus B and extends more or less in the general direction of the lobulus floccularis. In the majority of instances, these peduncles merge into the general medullary substance, and the only anatomic indication of an actual connection between the vermal folia and the folia of the lateral chain that can be determined is an indefinite ridge, which in many cases soon loses any degree of definition which it more centrally may have had.

The identification of the various fissures and sulci of the folial chain can be determined with considerable accuracy by identifying the fissures as they separate the various lobules of the arbor vitae and by following them outward into the folial chain. In most instances, this was fairly simple, although in the cetacea and in the elephant a clear differentiation between lobules was impossible on account of the fact that the folia making up the various lobules do not fall into clearcut

divisions, either mesially or laterally, since there are large folial masses in the depths of the fissures which form bridges between the preceding and succeeding lobules, and it is impossible to separate entirely the lobules without tearing across groups of submerged folia. In certain instances, the apparent separation of the lateral folia into lobules did not at all agree with the lobulation of the arbor vitae. This is particularly true of *Cetacea* in which the lobules of the lateral portion of the cerebellum are apparently connected with equal parts of preceding and succeeding arbor lobules, so that each lobulus of the arbor is connected with two lobuli in the lateral lobulation, and vice versa.

The folial chain. In general, the folial chain is fairly easy to follow, and, as emphasized by Bolk, it is continuous from the most cephalic folium of lobulus 1 to the most caudal folium of lobulus A, both in the vermis and in the hemisphere. In the parafloccular portion of the cerebellum, considerable difficulty arises in following the folial chain on account of the fact that in the depths of a fissure the chain may turn at right angles and proceed in most unexpected directions. A careful folium-by-folium investigation will, however, in all cases show the correct sequence of folia. The chain is complete, and not at any point is it impossible for one to follow the serial arrangement of the folial pattern.

In certain forms, an absolutely immediate connection between the termination of the lobulus parafloccularis and the beginning of the lobulus floccularis is difficult if not impossible to establish. This may be due to the fact that the lobulus parafloccularis is the most variable of all the portions of the lateral folial chain, and therefore some of its folia may be suppressed and a direct connection between the two not exist.

DETAILED DESCRIPTION OF THE ARBOR VITAE AND THE FOLIAL PATTERN IN CERTAIN OF THE MAMMALIA

The following descriptions are the result of a detailed examination of the arbor vitae and the folial pattern in the various animals which afforded the material for this study. In connection with the illustrations, in all cases the cephalic aspect is to the reader's left hand, while the caudal aspect is to his right, and the free surface of the cerebellum is away from the reader, while the neuraxial aspect is toward him. The arrangement of the folial pattern does not need any explanation, and a representation of the physical form of the animal in question

has been provided in order that there may be kept uppermost in mind the physical characteristics of the particular animal in connection with the pattern which his arbor vitae and folial chain present.

MACROPUS (KANGAROO)

The median section of the cerebellum of the kangaroo presents a comparatively circular outline, interrupted in its lower portion by a fairly wide open ventricular fastigium. The arbor vitae is divided into two fairly equal halves by the fissura primaria and the roof of the fourth ventricle, the two halves representing the anterior and posterior lobes. The fissura primaria is somewhat curved owing to the conformation of lobulus C, but it is essentially perpendicular as is also the fastigium which reaches the medullary substance. The fissura secunda is situated between lobuli B and C and divides the posterior lobe into a larger dorsal and a smaller ventral portion.

The medullary substance is disposed in the center of the cerebellum, being divided by the constriction produced by the approach of the fissura primaria to the ventricular fastigium, into an equally divided medullary substance of the anterior and posterior lobes. The prominent character of rays 4 and C 2 gives the impression of a U-shaped disposition of the medullary substance. The main mass of the medullary substance is almost horizontal, with a slight inclination upward and backward. The branches of the medullary substance are heavy, and there is a considerable degree of division of the medullary branches producing a moderately rich foliation.

The medullary rays

The first definite branch of the medullary substance ray 1 is a fairly robust stalk which arises from the under surface of the medullary substance, proceeds almost directly downward, giving off a few side branches, and terminates in a bifurcated extremity. Ray 2 is much heavier, comprising the entire extension forward of the medullary substance; it quickly divides into two major subdivisions, the first of which appears as a single stem which gives off a few lateral derivatives and ends in a branched extremity. The second branch, of about equal size, at once divides into two subdivisions which give off lateral branches. There is no ray 3. Ray 4 arises from the upper aspect of the medullary substance as a heavy stalk which almost immediately divides into two stems, ray 4 A and ray 4 B. The former proceeds forward and upward, giving off lateral branches, and ends in two rather elongated twigs. Ray 4 B proceeds more directly vertically and then arches forward, somewhat overhanging ray 4 A. It presents a small number of lateral branches and ends in a considerable spray. The medullary substance of the posterior lobe is heavy and gives rise to a number of stout branches. Ray C arises from the dorsocaudal angle, gives off a number of anterior unbranched prolongations and divides into a vertical C 2 and a horizontal C 1. Ray C 2 proceeds upward and forward, giving off undivided branches, and ends in an arched formation forward which somewhat overhangs lobulus 4. A well defined ray C 1 arises from the lower portion of C 2 and passes almost directly caudally, giving

off lateral branches. The caudal extremity of the medullary substance of the posterior lobe then gives rise to a single stout stem which almost immediately divides into two portions forming a subsidiary division, the upper being the simpler and giving off lateral branches, and the lower giving origin at its extremity to an extensive dendritic spray. Ray A arises close to the caudal extremity of the fastigium and consists of a slender branch which divides into a number of subsidiary twigs.

The lobules

The lobules as shown on the median section consist of a conspicuous lobulus 1, which forms the entire cephalic wall of the fastigium and presents a number of small folia. Lobulus 2 is divided into two definite subdivisions, corresponding with the two chief branches of the anterior extension of the medullary substance. Lobulus 4 is subdivided into lobulus 4 A and lobulus 4 B. Lobulus 4 A presents on its surface two chief folia which are rather broad. Lobulus 4 B is relatively slender, and simple in its deeper portion, but rather more complicated at its termination, undergoing a considerable degree of secondary division. Lobulus C 2 is relatively large, consisting chiefly of well defined folia, and forms the summit of the arbor vitae. Lobulus C 1 is simple and presents only three of four small folia on its surface. Lobulus B is subdivisible into a much larger ventral and a smaller dorsal portion, the larger ventral sublobulus dividing into a spray of subsidiary rays. Lobulus A is a simple structure forming the caudal limit of the fastigium and consists of only a few rather wide folia.

The folial pattern of Macropus

The folial pattern shows the division of the cerebellum into an anterior and a posterior lobe by means of the fissura primaria which arises at almost the midpoint of the median section of the vermis. It turns forward, however, thus separating a smaller anterior from a larger posterior lobe, and swings outward and forward toward the periphery of the hemisphere. The fissura secunda divides the vermis of the posterior lobe into a larger dorsal and a smaller ventral portion. It continues outward, limited throughout its entire extent by true folia, and limits caudally the lobulus paramedianus.

Lobulus 1 consists of four folia all of which are confined to the vermis except the most caudal one which shows a slight tendency to extend outward into the hemisphere. Lobulus 2 presents an easily recognized division into vermal and lateral portions. The cephalic and caudal folia do not extend as far laterally as the intermediate folia. Only two of the folia actually reach the periphery, and they are drawn together into a single peduncular root. Most of the folia show vermal subdivisions. Lobulus 4 presents two definite subsidiary portions. Lobulus 4 A consists of two broad folia which join before reaching the periphery. Lobulus 4 B is extensive on median section, but is drawn out laterally into a relatively condensed insertion into the medullary substance, the eight or ten vermal folia being reduced to two at the lateral extremity of the lobulus. This lobulus presents also a definite distinction between the vermal and lateral portions, evidenced by the swing forward and the limited extent of some of the secondary

sulci. Lobulus C is subdivided into a more extensive cephalic portion, lobulus C 2, and a less extensive caudal portion, lobulus C 1. Lobulus C 2 is rather extensive and consists of a series of vermal folia which are continuous laterally with a broad bare area of medullary substance crossed by broken sulci. The folia resume their normal appearance lateral to this denuded area as parallel laminae of gray matter, the most cephalic presenting a fairly simple arrangement corresponding to the position of the lobulus simplex. The mesial and lateral portions of this lobulus are barely continuous. Caudal to the lobulus simplex a fan-shaped arrangement of small submerged folia appears, which rather suddenly elongate forming a definite lobulus ansiformis, consisting of a relatively well developed crus 1 and crus 2. The two crura form a fairly definite sulcus intercruralis. The caudal portion of lobulus C 2 consists of a series of small folia which present a leaf-like arrangement arising from the bare connecting area and implanted by a single medullary peduncle into the white substance. These folia are succeeded by a series of laminae which rapidly increase in lateral extent until they reach the midline. Lobulus C 1 consists of a few vermal folia which extend outward as true folia to form the lobulus paramedianus. These folia are narrow, sinuous and somewhat irregular in arrangement. Lobulus C 1 and the lobulus paramedianus are thus confluent and do not present a definite demarcation in their vermal and lateral constituents. Lobulus B presents a collection of rather irregular vermal folia, which converge to form definite lateral extensions which come into close relationship with the paramedian formation and the inception of the lobulus parafoccularis. The lobulus parafoccularis consists of a number of folia arranged in rosettes which arise from a single stem and are applied to the lower and outer margin of the ansiform and paramedian formations. The lobulus parafoccularis turns backward to form a fairly definite but thick uncus terminalis. Lobulus A consists of two small subdivided folia which are continued outward as a single folium which is apparently continuous with the lobulus floccularis. The lobulus floccularis consists of six or seven small folia forming two rosettes which are situated between the parafoccularis and the cerebellar peduncle.

Lobulus 1 and lobulus 2 have independent peduncular implantations. Lobulus 4 presents a single implantation which chiefly serves lobulus 4 B. The lobulus ansiformis forms a large peduncle, as does also the lobulus paramedianus; while the lobulus parafoccularis possesses a separate implantation lateral and ventral to the preceding lobules.

Physical characteristics of Macropus

This kangaroo, about as large as a good-sized sheep, represents *Diprotodontia* and is a much more highly specialized form than *Thylacinus cynocephalus*, the representative of *Polyprotodontia*. The head is rather small, the eyes are situated well forward, possess overlapping fields of vision and are conjugated in their movements. In this and all other forms known up to the primates, the movements of the eyes are rather limited and are apt to be substituted for by movements of the head, the gaze being directed toward the object more by the movement of the head on the neck than by the actual change of axis of the eyes. The ears are prominent and are freely and independently movable. The jaws are not massive,

and the tongue is not prominent. The neck is rather short. The body is rather large and heavy, the thoracic portion being less massive than the abdominal segment. The limbs are disproportionate; the fore limbs are short and rudimentary, while the paws are well developed and capable of much pronation and supination. They function almost as hands, being capable of holding and also of a fair degree of unilateral independence. The hind limbs are excessively developed into extremely long and powerful extremities which are capable of propelling the kangaroo at a rapid pace. A large kangaroo can cover 26 feet at a stride when at high speed. When progressing slowly the kangaroo may go on all fours. When at high speed it leaps with both hind limbs acting together. It does not land on its fore limbs; these are tucked up against the thorax. In fighting with its adversaries the kangaroo will seize its opponent with its fore limbs and rip its enemy's body with the sharp claws of the hind limbs. It will also submerge its opponents with its fore limbs. There is little independence of the hind limbs. The tail is elongated and forms about two thirds of the length of the animal, heavy at its root and slightly tapering, and is used as a third leg of the tripod in the sitting position. When the animal is in motion, the tail has an extensive and efficient equilibratory and steering function. In standing, the kangaroo is supported entirely by the hind limbs so that it has an extensive need for equilibration, the body being fairly well balanced in its caudal half behind the limb support by means of the tail. In progressing, the kangaroo presents an extremely efficient equilibratory apparatus, being likely to propel itself 26 feet and land in a position which will at once allow another great leap. In the leaps, the tail is extended stiffly and acts efficiently as a counter-balance and also as a sort of rudder.

THYLACINUS CYNOCEPHALUS (TASMANIAN WOLF)

The general outline of the arbor vitae in the Tasmanian wolf presents a considerable degree of similarity to *Macropus*, being roughly quadrilateral in outline. It is not so equally divided into anterior and posterior lobes for in *Thylacinus* the posterior lobe has increased in size and apparently in importance. The division into anterior and posterior lobes is produced by the fissura primaria and the ventricular fastigium which have a distinctly oblique disposition from before downward and backward, the latter being in direct prolongation with the former. This arrangement apparently results from an increase in lobuli 2 and C. The general arrangement of the medullary substance is similar to that of *Macropus*, as it is constricted by the approach of the fissura primaria to the ventricular fastigium, and then expands into masses of considerable size in both the anterior and posterior lobes. It presents a distinctly U-shaped configuration through the extension upward of the relatively heavy rays 4 and C. The fissura secunda occupies relatively the same position as in the kangaroo, being situated between lobuli B and C. There is a definite increase in the size and complexity of the folia of the posterior lobe.

The medullary rays

The medullary rays are similar to those seen in the kangaroo. Ray 1 is a large heavy branch arising from the ventral surface of the medullary substance. It at once divides into two branches, the first being rather slender with a few side

branches and the second being heavier. Each of these subdivisions end in terminal bifurcations. Ray 2 consists of two stems the first being quite heavy and the second quite slender. Both these stalks undergo a rather simple division. Ray 3 is represented only by a small branch which lies in the depths and fails to reach the surface and appear in the folial pattern. Ray 4 is a long slender stalk inclined cephalad which gives rise to a major subdivision cephalically which forms the first part of lobulus 4. Its summit is somewhat less complicated than the summit of this ray in *Macropus*, but its caudal branches exert a definite influence on the folial pattern. Ray C is a thick heavy stem directed obliquely upward and back-

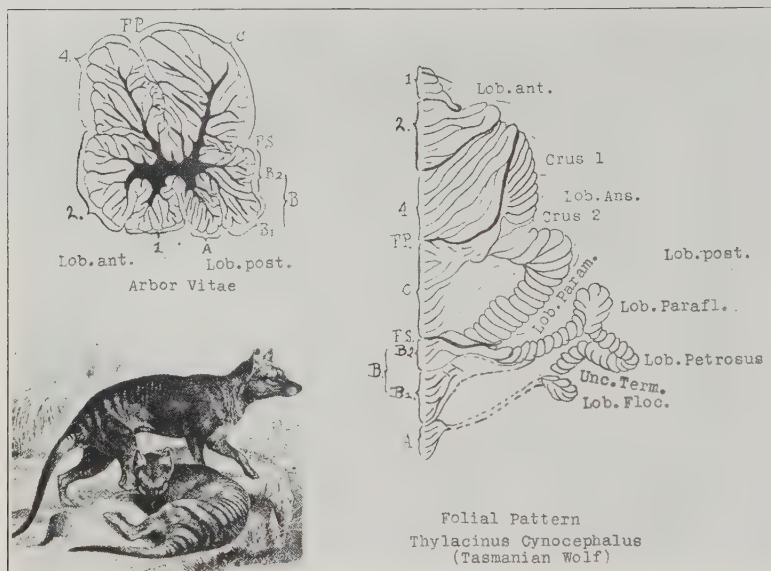


FIG. 4. *Thylacinus cynocephalus* (Tasmanian wolf), pouch dog

ward, and it is strongly developed cephalically, considerably overhanging ray 4. It gives off a number of long, slender cephalic branches, shorter, coarser caudal divisions and an apical spray. There does not appear to be a definite ray C 1, although the lowest branch in its divergent behavior in the folial pattern appears to be the homologue of ray C 1. Ray B presents an extensive development arising as a heavy caudal extension of the medullary substance which immediately divides into a rather complicated horizontal branch and a descending branch which is subdivided. Ray A is more complex than in *Macropus* showing a definite secondary branch proceeding caudally from a point near the origin of the ray.

The lobules

The lobular pattern is similar to *Macropus*, with the exception that a definite lobulus 3 does not develop. The ray which is the homologue of the ray forming lobulus 3 in *Macropus* appears to be incorporated with ray 4, so that lobulus 4 represents a consolidation of lobuli 3 and 4 as they appear in *Macropus*. Lobulus 1 consists of two rather simple groups of folia arising from a common stem. Lobulus 2 is composed of larger folia which fall into two groups. Lobulus 4 presents a distinctly conical appearance and consists of a cephalic group of folia corresponding to lobulus 3 and an apical group which also form the cephalic wall of the fissura primaria. Lobulus C is more extensively developed in its upper and cephalic portions and less so in its lower and caudal portion. Its apex is directed forward overhanging the fissura primaria and lobulus 4. It is somewhat suggestive in its morphology of the lobulus impendens, which is so conspicuous in certain of the rodent cerebella. Its upper portion is somewhat wider than its base. It is constituted mainly of rather broad folia. It does not show any definite division into sublobules C 1 and C 2, although the folial pattern shows a definite difference in the lateral extensions of the cephalic and caudal portions of the lobulus. Lobulus B is extensive being composed of two almost independent groups of folia—the upper group, lobulus B 2, being greater in number, more compact and shorter, as compared with those which form lobulus B 1. Lobulus A is well developed and presents in the depths of the fissure separating lobuli A and B a distinct caudal branch.

The folial pattern of Thylacinus cynocephalus

In the folial pattern, the fissura primaria has moved forward chiefly on account of the increased development of lobulus C. The fissura primaria swings outward, slightly backward and then almost directly forward forming a definite loop. The fissura secunda appears between lobuli C and B, and its lateral extension clearly delimits the lobulus paramedianus.

Lobulus 1 is represented by a number of small vermal folia the most caudal of which develops a lateral extension. Lobulus 2 presents a considerable number of vermal folia which suffer a great reduction in number as they are continued outward into the hemisphere. The folia are irregular in width and disposition. Lobulus 4 is definitely more developed than it is in *Macropus*, presenting a number of thin striplike folia which run forward and outward. There is some slight evidence of a vermal formation toward the midline in lobulus 4. The caudal portion of lobulus 4 shows the influence of the submerged folia seen in the depth of the fissura primaria which emerge on the surface in swinging lines more or less parallel with the fissure. Lobulus C is divided into two portions: A cephalic portion presents a definite vermal component, and then becomes constricted and is continued laterally into an irregular area which is marked by broken sulci. This area then expands as the lateral portion of the lobulus presenting a multi-foliated structure, forming crus 1 of the lobulus ansiformis. The caudal portion of lobulus C shows a definite vermal foliation which is succeeded by an undifferentiated area of bare medullary substance marked by a number of small broken irregular lines. Lateral to this bare area, the foliation again appears with the

development of a well defined crus 2. Crus 2 is then succeeded by a well defined lobulus paramedianus which bounds caudally the bare medullary area already mentioned. At the end of the lamellar chain forming the lobulus paramedianus a folium appears which is continuous with a submerged folium in the depths of the fissura secunda. This establishes a definite connection between the vermis and the lobulus paramedianus and fixes the position of the fissura secunda caudal to this folium. Lobulus B is subdivided into two portions: The cephalic portion shows definite vermal characteristics and is continued laterally by means of one or two wavy folia, with the lamellar chain forming the beginning of the lobulus parafoccularis. The caudal portion of lobulus B is vermal and shows a stalklike extension which is connected with the mesial extremity of the lobulus parafoccularis. The lobulus parafoccularis is directly continuous with the caudal termination of the lobulus paramedianus and continues forward as a chain of small folia which parallels the lobulus paramedianus and then develops a foliated rosette which encircles the apex of the lobulus ansiformis. This foliated structure then turns back on itself and gives out a lateral group of folia forming a definite lobulus petrosus and terminates as a well defined uncus terminalis. Lobulus A consists of a group of folia which is entirely vermal, but is connected with the base of the lobulus flocculus by an ill defined peduncle. The lobulus floccularis itself consists of a simple folial rosette situated between the lobulus parafoccularis and the cerebellar peduncle.

The implantation of the folia into the medullary substance laterally consists of a single peduncle for lobulus 1 and the cephalic portion of lobulus 2. The caudal portions of lobulus 2 and lobulus 4 are implanted by a single peduncle, while the lobulus ansiformis and the lobulus paramedianus rest on the medullary substance by means of a broad peduncle. The entire lobulus parafoccularis has a broad attachment to the medullary substance surrounding the implantation of the ansiform and paramedian formations.

Physical characteristics of Thylacinus cynocephalus

The Tasmanian wolf is a large wolf-like marsupial measuring about 4 feet from the nose to the root of the tail. It closely resembles the boar-hound in appearance, having a large, heavy head, rather short, mobile ears, a thick, short neck, four strong extremities adapted to a speedy running gait, a thick body and a doglike tail. It has a dentition typical of carnivorous animals, although not the same dental formula, strong heavy jaws and powerful teeth. The eyes are situated antero-laterally, possess overlapping fields of vision and are possessed of conjugated movement. This animal is essentially a quadrupedal mammal, the fore and hind limbs being used in progression equally. The gait is essentially doglike, a walk, trot or gallop. It is capable of considerable speed. There is no greater unilateral independence of the fore limbs than is manifested by the average dog. The Tasmanian wolf is a ferocious, combative, solitary animal, possessing a considerable degree of agility and grace in its movements.

BRADYPUS TRIDACTYLUS (THREE-TOED SLOTH)

The three-toed sloth presents a cerebellum of much more simple organization than its fellow representative of the edentate class, the anteater. The form of the

arbor vitae is simple, and irregularly circular. The branches forming the rays are relatively undifferentiated, presenting little secondary branching and little terminal arborization. The outline of the arbor vitae is irregular, each lobule standing out by itself, there being a considerable independence in the summits of the various lobes as the fissures cut rather deeply in between the lobules, thus isolating them from each other. The upper portion of lobulus C 3, however, presents a mushroomed-out appearance. The arbor vitae is divided into a smaller anterior lobe and a larger posterior lobe by the fissura primaria and the ventricular

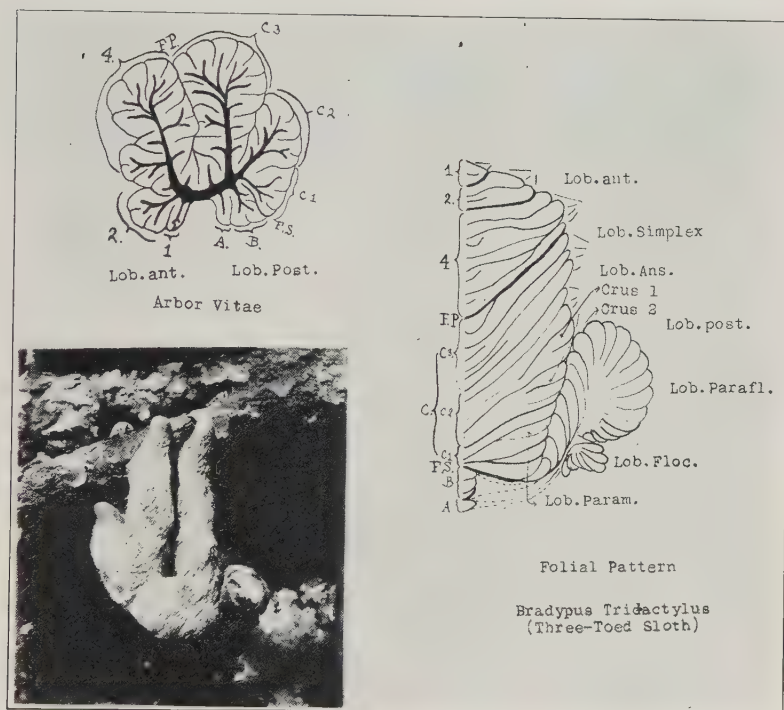


FIG. 5. *Bradypus tridactylus* (three-toed sloth)

fastigium. The fissura primaria is directed from before downward and somewhat backward, its termination directly approaching the ventricular fastigium which is wide open and directly limited cephalically by the medullary substance. The fissura secunda is situated as usual between lobuli B and C and is directed backward and markedly downward. The medullary substance is distributed more or less in the form of a thick arc lying directly above the ventricular fastigium, drawn out somewhat more into the posterior lobe than into the anterior lobe, and resembling a U through the well developed rays 4 and C 3. The branching takes place chiefly at the cephalic and caudal ends of the medullary substance.

The medullary rays

Ray 1 is a simple stem not possessing any lateral outgrowths. It bifurcates at the summit into two subrays. Ray 2 is a simple ray, which arises from the cephalic extremity of the medullary substance, gives off one lateral branch and then divides into two short terminal processes. There is no ray 3, although its homologue exists in a simple cephalic branch from the lower part of ray 4. Ray 4 is a relatively slight single stem which gives rise to a small number of lateral outgrowths which arise at almost right angles to the main stem, terminating in bifurcated extremities. There is practically no secondary division of any of these subrays. Ray C may be divided into two long rays, C 3 and C 2, and a shorter stem, ray C 1. Ray C 3 proceeds forward somewhat overhanging ray 4 which immediately precedes it. It presents only a few side shoots which are in turn meagerly subdivided. Ray C 2 is simple, arising as a direct caudal extension of the medullary substance and showing but little redivision. Ray C 1 arises from the base of ray C 2 and undergoes a simple subdivision. Ray B is composed of a single branch arising from the ventral extremity of the medullary substance, with only a few branches, and is directed chiefly downward. Ray A is a single, undivided small ray, lying immediately caudal to the ventricular fastigium.

The lobules

The lobules forming the arbor vitae are simple. Lobulus 1 presents a single, partially divided folium. Lobulus 2 presents only two broad folia, one of which shows a vernal subdivision. Lobulus 4 is separated considerably from lobulus 2, its folia are disposed almost at right angles to the central stem, are irregular and simple in their arrangement and not at all extensive. Lobulus C presents three portions, a lobulus C 3 which has some of the characteristics of the lobulus impendens of the cerebellum of the rodent, partially overhanging lobulus 4, a lobulus C 2 which is smaller than lobulus C 3, and a lobulus C 1 which is inconspicuous and really is only a part of lobulus C 2. Lobulus B appears as a relatively meager lobulus with only two surface folia. Lobulus A consists of a single folium forming the caudal wall of the fastigium.

The folial pattern of Bradypus tridactylus

The folial pattern on the sloth is the simplest found in any of this series, there being practically no lateral development and no ansiform formation worthy of the name. The folial pattern seems largely a simple extension of the vermis without any complications in the arrangement of the lamellae, each folium succeeding the preceding one in an almost uninterrupted series from lobulus 1 to lobulus C 1. The fissura primaria is rather cephalad to the midpoint of the folial pattern and proceeds forward and outward. The fissura secunda occupies its regular position between lobuli B and C, its lateral extension sharply delimiting the lobulus paramedianus which comes to a rather sudden termination.

The various lobuli show a simple arrangement. Lobulus 1 consists of a single folium which is subdivided only in the region immediately adjoining the midline. Lobulus 2 presents two folia which are subdivided in the median plane but which present definite evidence of lateral extension. Lobulus 4 shows a rather definite

differentiation into two portions: the cephalic portion is formed by two simple folia which are extended considerably laterally, while the succeeding three folia are subdivided mesially and do not extend as far laterally as does the cephalic portion.

Lobulus C presents a rather simple formation, divisible into sublobuli C 3, C 2 and C 1. Lobulus C 3 consists of three or four parallel surface folia which extend forward and outward. Lobulus C 2 is constituted by about five striplike surface folia, the middle three of which show a rudimentary attempt at the formation of a lobulus ansiformis. Lobulus C 1 presents a divergent group of folia representing the lobulus paramedianus. These folia radiate outward in a fanlike manner from the midline toward the periphery. Lobulus B consists of three small vermal folia connected by means of an ill defined peduncle with the lobulus parafoccularis. The lobulus parafoccularis appears as a direct continuation of the caudal termination of the folia forming lobulus C 1, producing a rather large wheel-like arrangement of lamellae proceeding forward and then returning upon itself, applied to the under and outer surface of the lateral portion of the hemisphere as far forward as the caudal portion of lobulus 4. Lobulus A consists of one small vermal folium which is connected apparently by means of an indefinite peduncle with a simple group of folia forming the lobulus floccularis, which appears as a folial rosette continued into a short lamellar chain.

The implantation of the folia into the medullary substance laterally follows a rather simple arrangement. Each one of the lobules of the anterior lobe and the subdivisions of lobulus C has a single independent peduncle. The parafoccular formation has a broad attachment ventral and lateral to lobulus C.

Physical characteristics of Bradypus tridactylus

The three-toed sloth is a peculiar, much specialized animal, which is almost blind and practically deaf. It is a sluggish creature, passing the greater part of its existence pendant from the limbs of trees or curled up with its head between its fore limbs. It is absolutely incapable, under any circumstances, of rapid, graceful movement. It wanders slowly and with excessive caution from limb to limb of trees. H. W. Bates states that the sloth is able to swim but he does not describe the swimming movements. When placed on its belly, the sloth sprawls out, and it can progress only with the greatest difficulty and slowness, crawling and dragging itself along with its claws, the soles of the feet being turned inward. The neck is short and mobile; the eyes are placed anteriorly with overlapping fields of vision; external ears are either rudimentary or not present. The limbs are adapted to a hanging position, the claws being curved in such a way as to favor the grip of the limb of the tree. In feeding, the sloth slowly and awkwardly drags leaves, twigs, etc., into its mouth with the fore limbs. The tail is only rudimentary.

MYRMECOPHAGA JUBATA (GREAT ANTEATER)

The form of the arbor vitae in the great anteater is definitely circular, with the exception of the irregularity in outline formed by the summit of ray C. The ventricular fastigium and the fissura primaria are not exactly opposite each other, the latter being situated somewhat caudal to the former. The fissura primaria is practically vertical. The fissura secunda appears between lobuli B and C, in

an almost directly horizontal position. The arbor vitae is divided by the fissura primaria and the ventricular fastigium, with a smaller anterior and a larger posterior lobe. In its general appearance, the cerebellum is a relatively highly differentiated organ. The rays are delicate, numerous and extensively branched. The medullary substance is more compact and is not drawn out into the stout stems which are seen in the marsupials and *Bradypus*. The amount of medullary substance is about equally divided between the anterior and posterior lobes in the center of the arbor vitae.

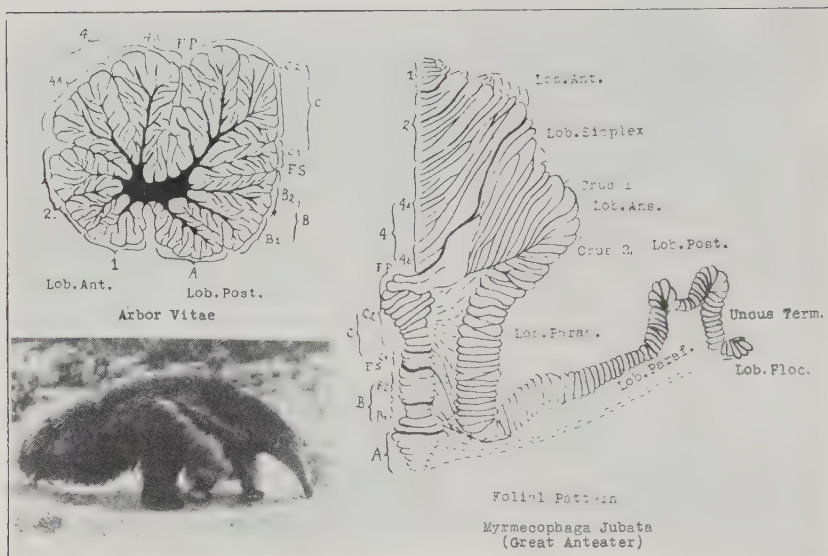


FIG. 6. *Myrmecophaga jubata* (great anteater)

The medullary rays

Ray 1 is highly developed. It consists of a strong single ray, which immediately branches into an anterior and posterior division. The rays forming the second lobulus in the anteater are situated in much the same position as these rays in the marsupials. They are, however, more richly subdivided, and the formation of the secondary folia is considerably greater than was the case in the preceding forms. There is no definite ray 3, ray 4 arising as a thick, heavy protrusion from the upper portion of the medullary substance of the anterior lobe, and almost immediately dividing into two strong rays, one of which proceeds forward and upward and the other almost directly upward. These both undergo repeated branching and each terminates by dividing into strong secondary divisions which again divide. Ray C is drawn out more caudally than it is in the marsupials. It gives off rami dorsally as it proceeds upward, and then ends by dividing into

two well developed terminal rays, the cephalic of which proceeds directly upward, dividing as it does so, while the caudal turns backward and then breaks up into a number of secondary rays presenting a peculiar conformation that is characteristic of all these forms in which the vermis presents a sinuous course. Ray C 1 appears as a relatively strong stalk arising from the base of ray C 2, not quite from the substance of the medullary mass itself, so that it cannot be considered as an independent branch, but must be considered as a part of lobulus C. This ray is separated from the succeeding ray by the fissura secunda. Ray B arises as two independent rays from the lower and caudal angle of the medullary substance. The lateral connections of these rays, however, show clearly that they constitute a single subdivision, since they are connected with the end of the lobulus paramedianus and the beginning of an extensive parafloccular formation. Ray A is well developed and presents a large number of dorsal and ventral branches which, in the main, bifurcate at their extremities.

The lobules

The lobulation of the arbor vitae is well organized, presenting a considerable degree of differentiation. Lobulus 1 is relatively extensive, consisting of two groups of folia. Lobulus 2 consists of two well developed subdivisions which are relatively richly foliated, the medullary rays being considerably subdivided. There is no lobulus 3. Lobulus 4 consists of two well defined divisions. These present a considerable number of folia, by far the greater number of which are hidden in the sulci. Lobulus C is subdivided into a rather extensive lobulus C 2, the caudal folia of which indicate the presence of a curve in the folial pattern and a lobulus C 1 which is narrow and contributes but little to the surface representation of the posterior lobe. Lobulus B is highly developed, being divided into two subsidiary lobules, which are richly subdivided and contribute very materially to the surface configuration of the posterior lobe. Lobulus A is well developed and consists of a considerable number of folia many of which lie in the fissure between lobuli A and B and also appear in the ventricular fastigium.

The folial pattern of Myrmecophaga jubata

The folial pattern presents a considerable increase in organization as compared with the marsupial pattern. The fissura primaria is well defined and appears at about the middle of the median section of the folial pattern. It extends forward and outward presenting a somewhat sinuous course. The fissura secunda appears somewhat above its usual position on account of the increased development of lobuli B and A. Its continuation, outward, however, may be traced to the usual point of transition between the lobulus paramedianus and the lobulus para-floccularis.

Lobulus 1 consists of four vernal folia and two caudal folia which appear to be somewhat independent. Lobulus 2 presents a subdivision into two definite portions both of which present definite vernal and lateral components. The foliation is rather simple. Lobulus 4 presents a rather considerable increase in complexity. It begins with two or three folia which extend throughout the entire width of the lateral hemisphere. Succeeding these, however, the folia of lobulus

4 A becomes shorter and shorter, the last folia being quite short and chiefly vermal in character. Lobulus 4 B is made up of three simple folia, two of which extend almost the entire width of the lateral hemisphere. Only one of these three folia, however, finally reaches the periphery. Lobulus C is divided into two portions, C 1 and C 2. Lobulus C 2 presents a peculiar formation of the first two visible folia, which leave the vermis as two narrow lamellae, become considerably widened and then contract to give rise to two simple folia which extend to the periphery representing the lobulus simplex. The succeeding vermal folia of lobulus C 2 form a simple twist of only about half a turn, straightening out to become continuous with the folial chain of lobuli C 1, B and A. The twisted and straight portions of C 2 connect in the depths of the paramedian sulcus with the folia which form the ansiform lobule. The lobulus ansiform succeeds directly on the folia forming the lobulus simplex, and consists of a group of shortening folia which pass laterally to form an apical transition from crus 1 into crus 2. Crus 1 and crus 2 produce a definite sulcus intercruralis. Crus 2 is succeeded by a straight paramedian formation possessing definite connections with the vermal portion of lobulus C 2. Lobulus C 1 presents a few vermal folia connected with the terminal paramedian folia. Lobulus B consists of two groups of serial folia, diminishing and then expanding in width as lobulus B 1 proceeds caudally toward lobulus A. The peduncle of lobulus B shows a definite inclination downward and outward around the elbow formed by the bend of the lobulus paramedianus, and seems to implant itself into the medullary substance supporting the lobulus parafoccularis. The lobulus parafoccularis consists of a long chain of lamellae that are directly continuous with the paramedian chain, closely paralleling its course in the reverse direction. When the parafoccular chain reaches the apex of the lobulus ansiformis, it turns mesially, then laterally and finally caudally, forming a fairly definite lobulus petrosus with an uncus terminalis. Lobulus A consists of a diminishing group of folia that are connected together into a peduncle which is continued outward toward the general region of the lobulus floccularis. The lobulus floccularis appears in the usual position between the parafoccular formation and the cerebellar peduncle.

The medullary implantations of the various lobules show that lobulus 1 and the cephalic portion of lobulus 2 have separate implantations, while the caudal portions of lobulus 2 and lobulus 4 have a common implantation. The lobulus simplex, lobulus ansiformis and lobulus paramedianus rest on a broad foundation of medullary substance, while lateral to it and separated from it by the sulcus parafoccularis, the parafoccular formation presents a long implantation into the medullary substance.

Physical characteristics of Myrmecophaga jubata

The great anteater is a large, bizarre-appearing animal varying in length from 4 to 7 feet. It is covered with stiff, bristly hair of considerable length, especially on the tail where it may be from 15 to 16 inches long. The head is elongated and narrow, the nose being considerably prolonged. The tongue is from 6 to 8 inches long, cylindric and extensible to a considerable distance. The eyes are antero-laterally placed and possess partially overlapping fields of vision; their movements

are not extensively conjugated. The ears are diminutive. The neck is long and mobile. The body is large and heavy and the limbs are of moderate length, the hind limbs being larger than the fore limbs. The hind limbs serve chiefly for locomotion. The fore limbs are capable of a limited degree of unilateral independence and are used not only for locomotion, but also for tearing to pieces the ant-hills where the animal's food supply is found. The fore limbs are also an efficient means of defense. In walking, the anteater curves the claws inward, the weight being carried on the outer sides of the forefeet while the hind feet are platigrade. It is not possessed of any degree of speed, its awkward progression being a sort of amble.

ELEPHAS ASIATICUS (ELEPHANT)

The arbor vitae of the Asiatic elephant provides a degree of foliation and subdivision that is rich even considering the complexity of the arbor vitae which is characteristic of the ungulate order. The primary divisions of the medullary substance are relatively complicated, and the secondary divisions exceed by far those found in any other of the ungulate group. The outline of the arbor vitae is more or less oval, the cephalo-caudad diameter exceeding the height of the cross-section. The fissura primaria lies in front of the median section of the arbor vitae almost directly opposite the approach of the ventricular fastigium to the medullary substance and is more or less curved, proceeding from before backward and downward. The fissura primaria and the ventricular fastigium divide the arbor vitae into the anterior and posterior lobes. The amount of substance provided by the posterior lobe considerably surpasses that furnished by the anterior lobe, about two thirds of the sagittal section belonging to the posterior lobe. The fissura secunda is relatively high in the circumference of the posterior lobe, and, instead of being more or less horizontal, it is directed at a considerable angle from before upward and backward. The fastigium approaches the medullary substance at about its midpoint and is deep and narrow. The main mass of the medullary substance is situated at the junction between the anterior and posterior lobes. It presents a rather blunt extremity extending forward into the anterior lobe with a crescentic disposition in the posterior lobe, there being a marked drawing upward of the medullary substance into ray C and backward into the rays forming lobulus B. All the chief branches of the medullary substance are heavy stemmed extensions from the medullary core, and they give rise to a profuse arborization.

The medullary rays

Ray 1 is of considerable size in comparison with those of the other ungulates, and it arises cephalad to the ventricular fastigium as a single trunk which gives off a considerable number of side branches and terminates in a bifurcation. The second branch arises independently from the medullary substance, but it probably belongs with the succeeding rami, the entire group representing ray 2, which forms a large lobulus 2. Ray 2 consists of this small independent branch which divides and gives origin to a large number of lateral branches, and of an extension

forward of the main mass of the medullary substance giving rise to two strong stems which proceed forward and upward giving off secondary divisions and bifurcating at their terminations. The uppermost of these is distinctly concave upward

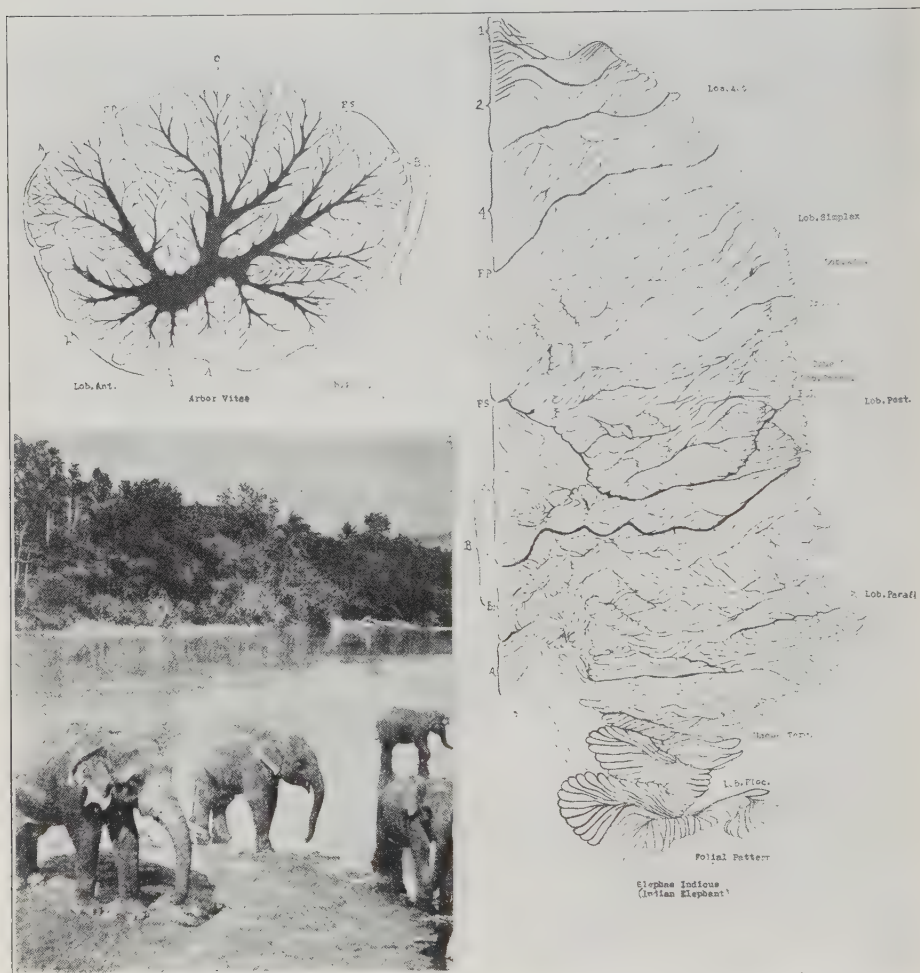


FIG. 7. *Elephas indicus* (Indian elephant)

and is heavily branched at its point of bifurcation giving off lateral branches and ending in a three-fold division. Ray 4 is a thick, heavy stem, arising from the upper aspect of the main mass of the medullary substance, giving off cephalic

branches and dividing into two strong stalks which proceed upward and forward, again subdividing and giving off numerous lateral branches. On its caudal aspect, ray 4 gives off a number of strong stems, particularly one in the depths of the fissura primaria, which forms part of the cephalic wall of this fissure. The medullary substance of the posterior lobe is concave upward and is continued backward into an ascending branch, forming ray C which gives off a number of small branches and then divides into a cephalic branch, which gives off a number of smaller twigs, and a large caudal branch, thick and heavy, which divides into three chief subdivisions. These subdivisions proceed upward and backward, giving off a large number of lateral twigs. In the depths of the fissura secunda, there is a strong branch near the base of ray C which is relatively heavy. In the folial pattern this branch gives rise to a paravermal extension which produces a cluster of folia. Ray B is a thick, prominent stem arising from the caudal extremity of the medullary core. It gives off two major subdivisions, an upper B 2 and a lower B 1, which subdivides into secondary and tertiary branches. Ray B 2 is extensive in the arbor vitae but much reduced in the folial pattern. It continues outward into a group of folia which forms what is apparently the first part of the paraflorculus. Ray B 1, although somewhat less extensive in the arbor pattern, has a much more extensive representation in the folial pattern, being connected with what is apparently the rest of the lobulus paraflorcularis. Ray A consists of a relatively slender stalk arising close to the ventricular fastigium and proceeding ventrally, giving off secondary branches.

The lobules

The lobules of the arbor vitae consist of the following: Lobulus 1 forms the cephalic boundary of the ventricular fastigium, and is composed of a number of close-set folia. Lobulus 2 appears as a triple lobulus consisting of an independent ray arising directly from the medullary substance, and two other groups of rays which arise from the main protrusion forward of the medullary substance, the dorsal ray being more extensive and divided into two portions. These lobules are all made up of a large number of secondary folia. Lobulus 4 is of moderate size and presents a number of deep branches and folia. It is composed of two chief groups of folia. The subsidiary subdivision is quite rich. Lobulus C is a relatively extensive lobulus consisting of a number of submerged groups of folia and four major groups which appear on the vermal surface. The subdivision into folia is relatively rich; many of the folia show a vermal division which does not extend out into the lateral lobe when the folial pattern is examined. Lobulus B is extensive, being subdivisible into two portions, lobulus B 2 and lobulus B 1. In the arbor, lobulus B 2 is more extensive than lobulus B 1, but the reverse is true in the folial pattern. Lobulus B 2 consists of three definite subdivisions, the dorsal two belonging together, and the ventral being more independent. Lobulus B 1 is complicated, being composed of a dorsal branch which is extensively subdivided, and a less highly developed ventral portion. Lobulus A is simple in its composition, being formed by a single undivided ray which gives off lateral branches. It forms the caudal boundary of the fastigium.

The folial pattern of the Asiatic elephant

The folial pattern of the elephant is extremely complicated. Its mass is by far the greatest of any cerebellum studied, and the richness of its foliation and the subdivisions far exceed those of any other form. The foliation is relatively irregular, folia appearing at many divergent angles at almost any part of the surface and terminating by merging into other folia or disappearing. The arrangement of the folia at the lateral extremities of the hemispheres is similar in *Elephas* to that in *Cetacea* in that there is a fusion in the depths between preceding and succeeding lobules. In general, as might be expected from the richness of the arborization in the arbor vitae, the folia are much more extensive in the midline than in the hemisphere, except in lobulus C and the lobulus parafloccularis, where the reverse is even more true; so that in the sum total the richness of foliation of the hemispheres exceeds that of the arbor vitae. All the lobules except C and B 1 show a tendency toward condensation as the periphery is approached. The most characteristic feature of the folial pattern of the Indian elephant is the consummation of the tendency which distinguishes the ungulate pattern, in the extrusion from the midline of a large number of folial rosettes which are disposed in a paravermian position, and which may well be described as the paravermis. This phenomenon appears only in the lobules beginning with the caudal half of lobulus C. The cephalic portion of lobulus C shows relatively the same arrangement of folia as is seen in the lobules of the anterior lobe, which indicates its agreement with the principles concerned in the formation of the lobulus simplex. A large number of sulci which appear in the vermis pass out only for a short distance. The majority of the fissures separating these lobules tend to run forward as well as outward. The fissura primaria is well forward in the folial pattern and divides the cerebellum into unequal divisions, the anterior lobe occupying a subordinate position, perhaps one fifth of the entire surface of the lateral hemisphere, and being characterized by a fairly simple folial arrangement.

Lobulus 1 consists of a group of about five surface folia, all of which show an increasing tendency toward the formation of lateral extensions. All of the folia of lobulus 2 show vermal characteristics and also participate in the formation of the hemisphere. The lateral extensions become more and more developed with each succeeding folium. The majority of the folia of lobulus 2 show a number of vermal sulci which converge into one narrow and one broad folium, which as they pass out into the hemisphere, are subdivided by a considerable number of lateral sulci. The second portion of lobulus 2 shows an essentially similar arrangement, a large number of vermal folia undergoing a considerable reduction in number at the midpoint of the hemisphere and a return to numerous lateral folia at the periphery. Lobulus 4 is a relatively simple lobulus, the folia of which are arranged more or less in parallel lines extending outward and converging on the periphery, the number of vermal folia being considerably reduced in the hemisphere. Lobulus C consists of two definite and distinctly differentiated portions. The cephalic portion shows an appearance similar to that seen in the anterior lobe, the folia being relatively simple, and the vermal portion presents practically no complications. At about the junction of the cephalic and middle thirds of lobulus C, however, both the vermis and the lateral portions begin to show a considerable degree of com-

plexity; the vermis presents a reduplication, and many groups of vermal folia are extruded laterally forming a series of folial rosettes lying along the paramedian sulcus which may well be termed the paravermis. The folia continuing outward from the vermis into the lateral hemisphere show an increasing degree of complexity, running at considerable angles. The great majority of the sulci run obliquely for only a short distance, disappearing into the fissures which limit the folial groups. Lobulus C shows a slight and abortive attempt to form an ansiform lobulus, there being only an unsatisfactory development of crus 1 and crus 2 and the intercrural sulcus. Following this irregular region there appears a group of folia which tend to arrange themselves serially from before backward and inward in the manner reminiscent of the formation of the lobulus paramedianus. Lobulus C is as usual bounded caudally by the fissura secunda. Lobulus B shows a definite division into cephalic and caudal portions. The cephalic portion is relatively extensive in the vermal region, producing an extremely complicated arrangement of the vermal rosetts in the paramedian fissure, but rapidly constricting as it extends outward until its lateral extension is reduced to only five or six striplike folia which continue outward and finally are reduced to a few lamellae. The remainder of the lobulus represented by lobulus B 1 is considerably less extensive in the vermis, but much greater in the hemisphere. This portion of the lateral hemisphere of the cerebellum, corresponding with the termination of the paramedian formation and the entire paraflocculus, presents a complicated arrangement of folia, it being almost impossible to follow the definite folial chain arrangement which has been so easy to trace and so characteristic of the folial pattern of the less complicated cerebella. The vermis shows the extrusion into the paramedian region of large groups of folia, and the root of the paraflocculus shows the production of a large number of folial rosetts which are continued outward into a series of folia which seem with some degree of complexity to follow one another in the usual chainlike arrangement. The paraflocculus gradually diminishes in size, the more cephalic lamellae being long narrow folia, constricts itself into what might be termed an uncus terminalis and terminates in close proximity to the lobulus floccularis which immediately succeeds it. Lobulus A is a simple group of folia forming a single rosette which has a definite peduncle continued outward in the general direction of the lobulus floccularis. The lobulus floccularis follows directly on the uncus terminalis of the lobulus parafloccularis and is situated in the usual position between the peduncle of the cerebellum and the termination of the lobulus parafloccularis. It consists of a sinuous series of moderately long, thin lamellae which are disposed in a double S-shape, the terminal folia being drawn out into a narrow chain which terminates in a roset that returns on itself.

- There is no definite arrangement for the peduncular implantation into the medullary substance. The entire development of the folia is so extensive that the medullary substance is tremendously increased, and the cerebellum is more or less evenly folded on itself along a simple furrow which is interposed between the lateral extremity of the anterior lobe and the lobulus simplex cephalically, and the remainder of the posterior lobe caudally. The furrow separating these insertions of the lateral terminations of the folia seems to terminate at about the separation between the folia assigned to crus 1 and to crus 2.

Physical characteristics of Elephas asiaticus

The elephant is the largest of all living mammals with the exception of *Cetacea*. It possesses a large, massive head, the nose being continued forward into a long actively mobile trunk which is used to explore the environment. The trunk is also prehensile and is used to obtain food and drink. The eyes are located in the sides of the head and possess to only a limited extent overlapping fields of vision and but little motility. The ears are rather large and possess a considerable range of movement. The neck is relatively short and thick. The tongue is pointed and movable within the mouth. The tusks are used for offense, and defense and also to dig up food. The body is large and heavy as are also the legs. The hind legs serve chiefly for locomotion. The fore limbs are used not only for locomotion but also to a certain extent with unilateral independence. The limbs are remarkable in the length of the upper segment. The elephant proceeds by walking or running and is capable of a speed of about 20 miles an hour. The tail is small and insignificant.

CAMELUS BACTRIANUS (BACTRIAN CAMEL)

The arbor vitae of the camel presents the same voluminous character which is to be seen in the other ungulates. The foliation is rich, and the arborization extensive. The entire arbor vitae seems to be drawn out in the cephalocaudal diameter. The chief distinguishing character of the arbor vitae is the enormously developed extension of the medullary substance forming ray C, which presents this particular form on account of the fact that lobulus C consists of a complicated series of loops, the medullary substance being accumulated on the surface of the peduncle of the loop. The arbor vitae shows the usual division into anterior and posterior lobes. The identity of the fissura primaria is clearly indicated by the depth of the fissure and the configuration of the medullary substance. The fissure, however, is situated considerably caudal to the midtransverse axis and approaches the fastigium of the fourth ventricle at a considerable angle. The fastigium is situated cephalad to the point of approximation of the fissura primaria. The fissura secunda is placed immediately behind a relatively small vermal lobulus C. The vermal portion of lobulus C is small on account of the fact that it presents an extensive curve, the major portion of the vermis being pushed outward to the right side and not appearing in the midline. Only a relatively inconsiderable part of lobulus C is represented in the median section. Lobulus B shows a considerable increase in size and also a marked lateral evagination to the right which, with the small size of lobulus C, seems to advance the fissura secunda more cephalad than is usual. The ventricular fastigium is relatively wide and comes into contact with the mass of the medullary substance at about a right angle.

The medullary substance is chiefly disposed as a large collected mass occupying the center of the anterior lobe and a long drawn-out tail which extends backward to form ray C. All the primary branches of the medullary substance are rather heavy and undergo secondary and tertiary divisions.

The medullary rays

Ray 1 is relatively heavy, arising from the under part of the first portion of the medullary substance and presenting a stout cephalic branch immediately after its origin. Ray 2 arises as the cephalic prolongation of the medullary substance and consists of two chief branches which undergo considerable subdivision. Ray 4 divides into two rather definite groups, the first two forming lobulus 4 A. They consist of two fairly slender independent fasciculi which pass forward and upward from the dorsal prolongation of the medullary substance. Ray 4 B appears as a

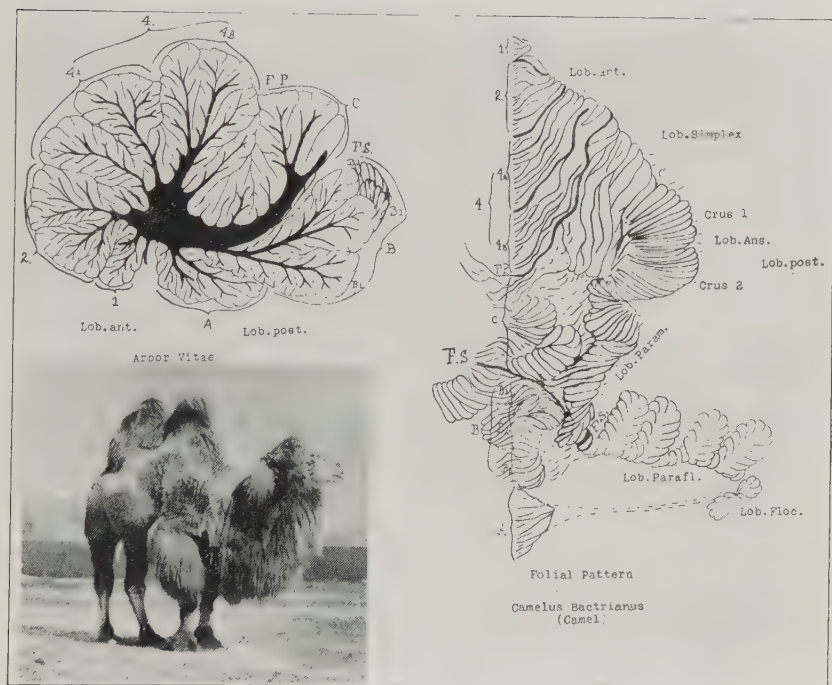


FIG. 8. *Camelus bactrianus* (Bactrian camel)

thick vertical branch, which rapidly divides into three subsidiary rays, and a long slender branch, which arises from the junction of the dorsal prolongation of the medullary substance with the main mass. All these rays undergo a rather rich division, and the foliation of the lobulus is extensive and complex.

The mass of the medullary substance in the posterior lobe is relatively extensive but consists chiefly of a long drawn-out extension which forms the superficial core of lobulus C. The other medullary rays are relatively slender. From the concave upper surface of ray C there arise a number of elongated branches which

lie in the depths of the fissura primaria. The summit of ray C divides into three main branches: the first two are situated more or less in the sagittal plane, the more cephalic giving rise to a number of twigs, while the third represents a transverse extension outward of the medullary substance as a peduncle for the remainder of the convoluted portion of lobulus C and presents the characteristic appearance of the medullary core of a twisted vermis. It is covered by a thin layer of cortical substance caudally. There is not much secondary division in ray C. Ray B is a relatively stout fasciculus which divides almost immediately into two subdivisions. The dorsal one undergoes further subdivisions, so that there are three definite subdivisions of ray B, the most cephalic of which is relatively simple and lies chiefly in the midline, representing the median vermis. The second portion is rather complicated. It extends outward and forward in an imbricated series of folia presenting a double tier of folia overhanging the first branch of ray B. It is shown clearly in the folial pattern as a leaflike extension which is squeezed out from the midline and lies to the right of the midline. The most caudal division of ray B is a simple vermal formation which, however, again lies chiefly on the right side. It presents a series of bifurcated branches. Ray A is a heavy fasciculus arising from the under and cephalic extremity of the posterior medullary substance and immediately dividing into two branches which undergo secondary division.

The lobules

The appearance of the arbor vitae indicating that the anterior lobe is more extensive than the posterior lobe is misleading, for the folial pattern shows that the vermis of the posterior lobe is much more extensive on account of the vermal reduplications which force the major portion of the vermis into a paravermian position and thus reduce the midline vermis. Lobulus 1 is a fairly well defined lobulus, cephalically limiting the fastigium, arising from a portion of the superior medullary velum and thus possessing some lingular characteristics. It presents one definite subdivision which lies in the sulcus between the first and second lobuli. The importance of this submerged branch is that it is continuous with a folium which extends outward and shows a definite lateral extension almost incorporating itself with the folia of the lobulus 2. Lobulus 2 is fairly extensive, presenting two major subdivisions and a series of minor subdivisions totalling five folial groups. Lobulus 4 is extensive, presenting two definite portions: a cephalic portion supported by two medullary rays and a caudal portion developed on one heavy ray which presents a number of surface reduplications forming the summit of the arboreal pattern and a number of subsidiary rays in the depths of the fissura primaria. Lobulus C is not extensive in the midline. Its cephalic portion is relatively simple and presents the usual crosscut appearance of the arbor, while its caudal portion presents a heavy extension of the medullary substance which indicates the function of this part of the medullary ray as a peduncle for the lateral extensions of the lobulus. Lobulus B presents three separate portions. The dorsal portion is relatively simple and is confined chiefly to the midline; a second portion shows a marked lateral extrusion in the paravermian region, and a third again returns to the midline and is relatively simple. Lobulus A is subdivided into two portions. It forms the caudal limit of the ventricular fastigium.

The folial pattern of Camelus bactrianus

The pattern of the camel is complicated. The division of the folial pattern into anterior and posterior lobes shows a marked subservience of the cephalic group to the much increased mass of the caudal group of lobules. The anterior lobe shows an orderly arrangement of folia in parallel lines, with a definite vermal division characterized by short sulci passing out from the midline indicating a definite paravermal depression. The lateral extensions increase from before backward. The lateral folia are narrow and more numerous near the midline tending to decrease in number as the periphery of the hemisphere is approached. In general, all the lines of the anterior lobe tend to converge. The fissura primaria is an easily recognized fissure beginning at the midline and presenting a rather sinuous course as it runs forward and outward toward the periphery. The posterior lobe shows a marked complexity in the organization of the vermis which is carried to such an extent that more of the vermis exists in a paravermian position than actually in the midline. The lateral extensions are prominent and present a rather complicated arrangement particularly in the region of the ansiform and paramedian formations. The fissura secunda is readily distinguishable between the vermal lobuli B and C, and appears in the lateral pattern at about the junction of the paramedian formation with the lobulus parafloccularis.

The first lobule consists of three vermal folia which converge into a definite independent peduncle, and a folium which arises from the depths of the fissure between the first and second lobuli and extends outward as a definite lateral extension, incorporating itself with the folia of the second lobulus. Lobulus 2 is relatively complicated. The sulci outlining the folia present a sinuous course. There are a number of short subsidiary vermal divisions. The lateral extensions increase in length from before backward and tend to converge into a single peduncle with which the lateral extension from lobulus 1 incorporates itself. There is a single medullary implantation for lobulus 2. Lobulus 4 presents a division into cephalic and caudal portions. The cephalic is rather more extensive from before backward, while the width of the caudal portion is greater. The same short sulci appear in the vermal region, indicating a definite vermis and a definite lateral expansion. The folia tend to converge, so that the extent of this lobulus in the periphery is considerably less than it is in the midline. The cephalic portion is continuous with the caudal portion at the periphery, there being a common folium belonging to both. There is a single medullary peduncle for the fourth lobulus. Lobulus C presents two definite portions, a simple vermal cephalic part and a convoluted paravermal caudal division. The first group of folia extends for only a short distance and then gives way to a formless large folium crossed by broken sulci emerging from the fissura primaria but soon returning to the depths of the same fissure. A number of fairly straight folia which extend outward and correspond to the lobulus simplex appear to be connected with this part of the cerebellum. The second paravermal portion of lobulus C consists of a marked curve to the right comprised of two groups of folia drawn together in a peduncle. The peduncle of the caudal part of this curve forms a definite mass and represents the broad medullary substance of ray C seen in cross-section in the caudal portion of lobulus C. The hemispheric part of lobulus C consists of a series of folia which

are not directly continuous with the vermal folia, a wide area of almost bare medullary substance being interposed. This is crossed by a number of finely marked lines representing some attempt toward folial formation. The lateral folia consist of a number of fairly regularly disposed lamellae which succeed one another passing outward. These soon give way to a definite ansiform formation with a large number of short folia converging on a peduncle which is continuous with the bare mass of the medullary substance interposed between the vermis and the hemisphere. The lobulus ansiformis presents a definite crus 1 and a crus 2 which, before its transformation into the paramedian formation, presents a marked folial roset. The lobulus paramedianus, as it develops caudal to the roset marking the termination of crus 2, forms at once another roset made up of folia, the base of which is directed laterally—there then appear a number of narrow folia which are followed by a rather rapidly widening group of lamellae, the widest of which are insinuated in the depths of the fissura secunda and form the rudimentary folia which appear in the caudal aspect of ray C. The lamellae narrow and form finally a fairly prominent roset which terminates the lobulus paramedianus. The caudal folia of crus 2 and the folia cephalad to the wide folia which disappear in the fissura secunda are connected with the vermal folia of lobulus C by means of the wide bare medullary area already mentioned. The group of folia in the middle of the lobulus paramedianus which is directly continuous with the vermal folia shows a similar formation on the left side of the vermis, which is continuous with the lower end of the paramedian formation of the left lateral lobe. Lobulus B is subdivided into three subsidiary portions, the first portion consisting of a group of folia which represent a curve of the vermis to the left and its return to the right. These folia then rather sharply turn to the left side of the vermis, and as suddenly return to the right, producing 2, marked folial roset which corresponds with the overhanging portion of lobulus B 2, as seen in the arbor vitae. The folial chain then gradually returns to the midline, representing the rest of the middle portion of lobulus B. The last portion of lobulus B is similar to the first portion and consists of a group of successive median folia of which, however, are also disposed chiefly on the right side of the midline. All the folia of lobulus B converge on a peduncle which tends to run outward in the usual position toward the base of the lobulus parafloccularis. The lobulus parafloccularis consists of a series of folial clusters rapidly succeeding one another and connected by only an insignificant number of short folia. This group of folial clusters occupies the usual position in the lateral hemisphere, ventral and lateral to the lobulus paramedianus and the lobulus ansiformis, extending well forward toward the origin of crus 1. There is no definite uncus terminalis and no lobulus petrosus. Lobulus A consists of a series of simple folia, symmetrically arranged and presenting vermal sulci without lateral extensions, which converge on a single peduncle. This peduncle runs out and fades away into the medullary substance more or less in the direction of the lobulus floccularis. The lobulus floccularis consists of a double group of folia which do not possess a visible connection with the lobulus parafloccularis. The lobulus floccularis appears in the usual position lying between the cerebellar peduncle and the parafloccular formation. The lobulus simplex, lobulus ansiformis and lobulus paramedianus find a broad insertion into the medullary substance by a series of implantations. The lobulus parafloccularis is based on the medullary substance lateral and ventral to the preceding lobules surrounding, to a certain extent, the insertion of the ansiform and paramedian formations.

Physical characteristics of Camelus bactrianus

The camel is an ungulate of considerable size, with a somewhat elongated body, four moderately long and slender legs, a long neck and a rather large head. The tongue is fairly long and quite mobile, and it is used to draw food into the mouth. The lips are large and fleshy, the upper being actively prehensile. The eyes are situated on the sides of the head and possess overlapping fields of vision only to a limited extent; they are only slightly mobile and are conjugated in their movements. The ears are small and rounded. The neck is long and freely mobile. The camel uses the mouth and teeth as means of defense or offense. It also will roll on its enemies if they are small. The limbs are used almost exclusively for locomotion, the particular footpad development adapting it to walking in sand. The body is large. The tail is small and inconspicuous. The gait of the camel is a slow shuffling walk or trot which can be increased to a lumbering awkward gallop. There is practically no unilateral independence of the fore or hind limbs.

RANGIFER TARANDUS (REINDEER)

The ungulates, in general, present a relatively similar type of cerebellar organization. The development of the cerebellum is particularly marked in the vermis which is extremely massive and presents a considerable degree of subdivision. The chief mass of the cerebellar organization is in the midline. The arbor vitae presents a complicated appearance, the lamellae being numerous and the medullary rays stoutly developed and presenting a considerable degree of secondary division and reduplication. The outline of the arbor vitae of the reindeer is more or less elongated and quadrilateral, the cephalic being somewhat more rounded than the caudal portion. The ventricular fastigium and the fissura primaria are almost directly opposite one another. The fissura primaria is perpendicular, inclining slightly from before backward and downward. The ventricular fastigium is narrow and relatively deep. The anterior lobe occupies distinctly less of the surface of the arbor vitae than the posterior lobe. The fissura secunda appears low in the posterior lobe separating lobuli B and C, on account of the considerable increase in the complexity of lobulus C. The medullary substance presents a rather condensed protrusion forward into the anterior lobe and is drawn out caudally into a long, stout, well developed branch which turns upward into lobulus C, giving off successive branches as it proceeds backward and then turns upward. There is a relatively large number of submerged folia of considerable size, particularly in the depths of the fissura primaria.

The medullary rays

Ray 1 has no definite origin from the medullary substance but appears more or less in the form of a lingular development. The successive medullary twigs appear not to originate in any definite stem but seem to arise from the superior medullary velum. Ray 2 is a conical prolongation of the medullary substance forward which gives rise to a series of branches on its ventral surface at right angles to the medullary mass, which present a fair degree of secondary division. The final stem of

ray 2 is a direct prolongation forward of the medullary mass and divides into a terminal group of three subsidiary branches. There is no ray 3, although it is suggested by a submerged single folium arising near the base of ray 4. Ray 4 is a heavy stem arising at an angle from the medullary substance and directed forward and upward. At a considerable distance from its origin, it gives rise to a strong prolongation forward which rapidly subdivides forming a distinct subray 4 A. The rest of the ray continues upward, giving off lateral offshoots, and finally subdivides as it approaches the summit. There are a number of well developed

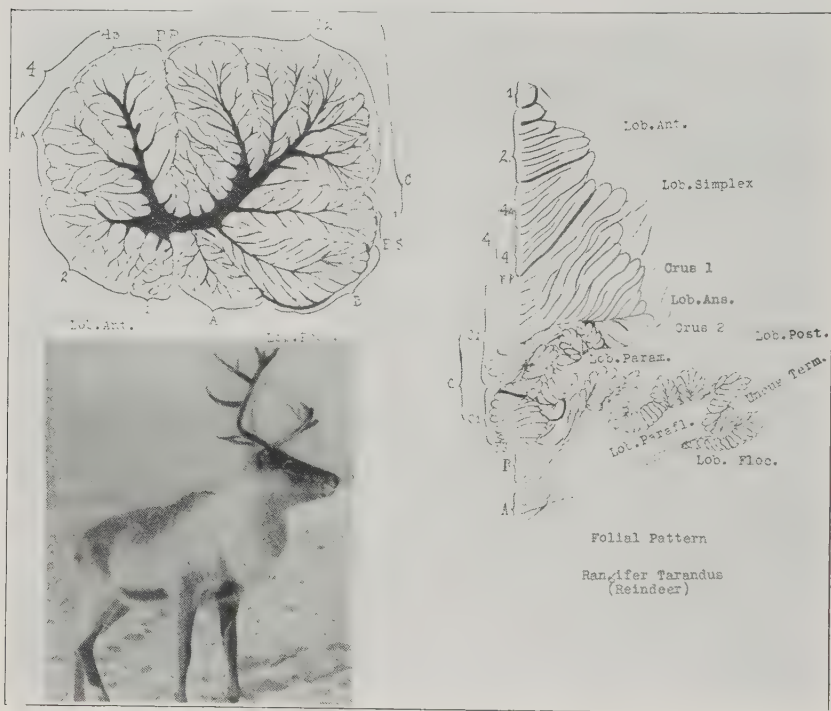


FIG. 9. *Rangifer tarandus* (reindeer)

slender rays along the caudal aspect of ray 4 B which form a group of folia submerged in the fissura primaria. This same arrangement of well developed submerged folia is found along the cephalic aspect of ray C 2. Ray C 2 is a large heavy ray and appears as a direct prolongation backward of the medullary substance of the posterior lobe. It gives origin, as already mentioned, to a number of slender rays whose folia are completely submerged in the depths of the fissura primaria. It continues backward and gives rise to a large, heavy ray which curves upward and forward, sending its subsidiary branches forward toward the fissura

primaria. There is a large number of these cephalic and caudal subsidiary rays, the majority of which bifurcate at their extremities. Continuing upward and backward, ray C 2 then gives rise to a slender dorsal ray which is richly branched and presents a terminal subdivision. The terminal portion of ray C 2 continues backward into a gradually diminishing ray which sends branches upward and backward to form an apical spray, before doing which it gives rise on its caudal surface to two rather well developed rays which present in the arrangement of their ventral folia, particularly the lower one, the typical appearance shown by folia which are cut at an angle. These rays enter into the formation of the convoluted vermal folial arrangement characteristic of the caudal portion of ray C 2 and the beginning of ray C 1. The caudal aspect of the lower part of ray C 2 gives origin to one or two slender folia which serve to connect the convoluted folial pattern of one side with folia of the other side. Ray C 1 arises near the base of ray C 2 as a slender dorsal branch, which gives rise to simple lateral branches and then bifurcates. Ray B is a long curved branch from the caudal angle of the medullary substance which presents numerous lateral outgrowths. Ray A is a relatively slender ray, which, however, is richly branched and presents a number of subsidiary folial groups.

The lobules

Lobulus 1 presents a peculiar organization, not having a central ray, but it is provided with a number of slender twigs which appear to arise from the superior medullary velum. Its peripheral portion is considerably broader than its proximal origin from the medullary substance immediately adjacent to the ventricular fastigium. This arrangement may be considered to be a true lingual. Lobulus 2 arises on the basis of a number of medullary rays, the first two of which seem to spring by independent origin from the medullary substance. The medullary core extends forward to a conical termination which affords origin for three subgroups of folia, the entire lobulus being made up of seven folial groups, the first and last being submerged from the surface, and the remaining five appearing on the surface. The junction of lobulus 2 with lobulus 4 presents an indentation as if produced by the mesencephalic collicular plate. Lobulus 4 is made up of two subsidiary groups produced by the division of ray 4 and presents a simple series of folia. Lobulus C is rich and extensive, being subdivided into a complicated lobulus C 2 and a simple lobulus C 1. Lobulus C 2 consists of two portions. Its cephalic portion is relatively simple corresponding with a similar simple arrangement in the folial pattern. Its caudal portion, however, made up of the complicated terminal efflorescence of ray C 2, is much more highly developed, and in its caudal division shows that the vermis is undergoing a series of twists from one side to the other. Lobulus C 1 is relatively narrow and simple in its organization, as the vermal twisting has ceased in this part of the cerebellum. Lobulus B is rather extensive and bulbous, the surface folia showing no complexity in arrangement. Lobulus A is, again, of a peculiar shape, expanding considerably and having a relatively simple surface expression.

The folial pattern of Rangifer tarandus

The folial pattern of the reindeer shows the increasing predominance of the posterior lobe. The anterior lobe is relatively simple. The fissura primaria appears somewhat cephalad to the midpoint of the sagittal section, is directed markedly forward and outward and is relatively straight. The fissura secunda appears between the complicated convolutions of lobulus C and the relatively simple arrangement of lobuli B and A. It is continued laterally and limits the lobulus paramedianus at its junction with the parafoccular formation. Lobulus 1 presents a few vermal lamellae. Lobulus 2 consists of two relatively short lamellae which are succeeded by three parallel folia which are all subdivided in the vermal region and show distinct evidence of participation in the formation of the lateral mass. The folia of lobulus 4 are relatively simple in arrangement, being successive lamellae with a vermal differentiation, two, three or four folia joining to form a single folium as it approaches the lateral extremity of the hemisphere. Lobulus C presents a division into lobuli C 2 and C 1 which, again, are subject to considerable resubdivision. Lobulus C 2 presents a simple cephalic portion, consisting of parallel folia which extend from the mesial to the lateral limit of the hemisphere. There is a definite division between a vermal and a lateral portion. The most cephalic folia of C 2 represent the lobulus simplex. There are a number of shorter folia succeeding the lobulus simplex, followed by crus 1 of the lobulus ansiformis, a successive chain of shortening lamellae. Crus 1 forms a distinct apex, with the appearance of a short crus 2 and the production of a definite sulcus interculturalis. Before the transition into the lobulus paramedianus, the folial chain presents a double rosette which is then succeeded by the regularly arranged folia of the lobulus paramedianus.

The vermal portion of lobulus C 2 connected with the lobulus ansiformis and the cephalic part of the paramedian formation shows a marked convolution. The lamellar chain begins on the right side of the vermis, but extends more and more to the left, the first turn of the sigmoid arrangement occurring practically entirely on the left side of the vermis. Following this, the lamellae return to the right side, creating a distinct S-shaped formation, with the second loop of the S entirely on the right side of the midline. The lamellae then approach the midline, extend partially into the left side of the vermis and then gradually return to the median position. The middle folia of C 1 come into direct relationship with the terminal folia of the lobulus paramedianus. The caudal folia of lobulus C 1 are connected with the lobulus paramedianus by means of a peduncle. Lobulus B is a single roset with a peduncle which is continued outward toward the base of the lobulus parafoccularis. The lobulus parafoccularis appears as a direct continuation of the paramedian chain, almost at once developing a series of lamellar rosettes. This chain of parafoccular rosettes is continued around the under and outer surface of the lobulus ansiformis as far forward as the lobulus simplex. At this point, the chain turns on itself and returns along its proximal arm, terminating as a fairly well defined uncus terminalis. Lobulus A consists of a relatively simple rosette, the peduncle being continued outward toward the termination of the lobulus floccularis. The lobulus floccularis consists of a chain of lamellae, gradually increasing in size until it terminates in a rosette.

The reindeer presents a lingula which possesses a lateral implantation that serves also for the most cephalic folium of lobulus 2. There is an independent peduncle for the remainder of lobulus 2 and also for lobulus 4. Lobulus C has a single broad implantation with the parafloccular implantation lateral and ventral to lobulus C.

Physical characteristics of Rangifer tarandus

The reindeer presents the typical form of the deer, being fairly heavily built, with four moderately short legs, a long neck, a good sized head and spreading antlers. The eyes are situated well forward in the head and have considerably overlapping visual fields. The movements of the eyes are well conjugated and present a considerable range of mobility. The tongue is large, fleshy and prehensile. The neck is fairly movable. The body is of medium weight and the legs are slender and rather short, with padded feet. The tail is almost nonexistent. The reindeer advances by walking, trotting and running. It is possessed of a considerable degree of speed but does not present any material agility or nimbleness. There is little unilateral independence in the use of its forefeet.

GIRAFFA CAMELOPARDALIS (GIRAFFE)

The pattern of the arbor vitae of the giraffe shows the extreme degree of differentiation and division which is typical of the ungulates. The arbor vitae is roughly quadrilateral in shape and presents a considerable notch in its cephalic border in which is lodged the collicular plate of the midbrain. The arbor vitae shows the usual differentiation into anterior and posterior lobes by the fissura primaria and the ventricular fastigium. The fissura primaria appears directed from above downward and somewhat forward, approaching almost directly the summit of the ventricular fastigium. The fastigium is a long narrow recess which extends upward to the medullary substance. The fissura secunda appears in its usual position between lobuli B and C, directed from before backward, and somewhat upward. The posterior lobe is considerably larger than the anterior lobe, while the fissura secunda divides the posterior lobe into a greater dorsal and a smaller ventral portion. The arrangement of the medullary substance in the center of the arbor vitae presents a U-shaped form, owing to the heavy character of rays 4 B and C 2. The rest of the medullary substance is situated in the center, that of the anterior lobe being relatively large and divided into two portions. One corresponds to the extension forward of the medullary substance, while the second is an upright stalk forming the base for ray 4. The medullary substance of the posterior lobe is drawn out into a curved caudal extension which gives origin to the large rays forming lobuli C 1 and C 2. The arbor vitae is characterized by the extreme richness of subdivision, a large number of secondary and tertiary medullary branches arising from the chief divisions.

The medullary rays

Ray 1 arises as a sort of lingular formation from the depths of the fastigium by a branch which springs from the junction of the superior medullary velum and the

medullary substance, then frees itself from the former, forming an independent ray. The medullary rays of lobulus 2 form a series of separate independent stalks arising from the stubby cephalic projection of the medullary substance. These rays are three in number. The first is a simple stem giving off lateral branches. The second is thicker, gives off lateral stalks and is subdivided. A small submerged ray follows. The third stem, the largest of the three rays, appears as a direct continuation forward of the medullary substance and is a relatively thick stalk which divides into two main subdivisions which give off lateral branches and

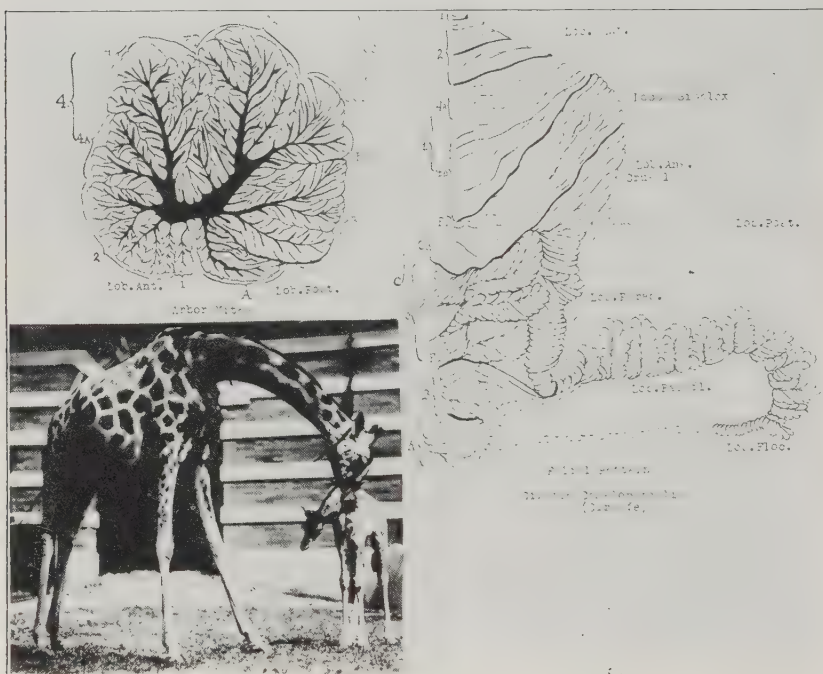


FIG. 10. *Giraffa camelopardalis* (giraffe)

undergo further division. Ray 4 appears as a thick, heavy vertical extension of the medullary substance which immediately divides into two heavy rays, the cephalic extending forward and then subdividing to give origin to a number of smaller branches. Ray 4 B proceeds almost directly upward as a thick, heavy stem, giving off short cephalic branches and a longer stalk which somewhat overhangs lobulus 4 A. The termination of ray 4 B proceeds upward to divide into a spray of subsidiary branches. A considerable number of long branches arise from the caudal aspect of ray 4 B and lie in the depths of the fissura primaria. These become simpler as the depths of the fissura primaria are approached, the

uppermost showing a secondary subdivision; the second only lateral branches, and the third no branches at all. There are a number of short rays in the depths of the fissura primaria which apparently belong to the posterior lobe. Ray C arises as a thick heavy continuation upward and backward of the posterior medullary substance. It is large and gives off a series of rays situated in the depths of the fissura primaria, some of which are rather richly branched, and then divides into ray C 2 and ray C 1. Ray C 2 almost at once gives rise caudally to a long, curving plumelike ray and a thick, heavy vertical stalk cephalically, which then subdivides into a number of complicated branches. Ray C 1 proceeds backward as a relatively heavy ray, giving off lateral branches, and then subdivides in a manner characteristic of a considerable degree of convolution in the vermal pattern. In the fissura secunda are a number of subsidiary rays, one of which is of considerable size and apparently participates in the marked reduplication of the vermis. Ray B arises as a direct continuation backward of the posterior medullary substance, giving off a few short branches, and then subdivides into a dorsal and ventral branch, the former being quite complicated. Ray A arises from the medullary substance close to the fastigium, proceeding directly downward and then backward in a long curve, giving off a considerable number of short cephalic branches and a large number of long drawn-out caudal branches.

The lobules

The lobules of the arbor vitae depend on the complicated medullary division. Lobulus 1 consists of a narrow group of folia attached at its base to the superior medullary velum. Lobulus 2 consists of three primary divisions which may be resolved into at least seven subsidiary surface lobules. The first is an undivided lobulus, the second divides into two while the third is composed of four sub-lobules. Lobulus 4 A shows the effect of the collicular plate of the midbrain in its external configuration and consists of two simple divisions. Lobulus 4 B presents the cephalic summit of the arbor vitae. It has a rather complicated arrangement, owing to the large size of the sublobules which form the upper part of the cephalic wall of the fissura primaria. Lobulus C is a voluminous lobe, many branches being hidden in the depths of the fissura primaria. It is subdivided into two portions, lobuli C 2 and C 1. The caudal portion of lobulus C 2 presents a long plumelike lobulus already mentioned in the depths of the sulcus between lobuli C 2 and C 1, participating in the formation of the lateral swing of the folia into the left side of the vermis. Lobulus C 1 presents the usual appearance of a lobulus sectioned while in the process of a twist or turn in the formation of the vermal folial pattern. Lobulus B consists of a larger dorsal portion and a simpler ventral division. In the depths of the fissura secunda appear a number of subsidiary folia which participate in the swing of the vermal chain to either one or the other side. Lobulus A presents a peculiar long drawnout appearance with a large number of folia which are hidden in the depths of the fissure separating lobuli A and B.

The folial pattern of Giraffa camelopardalis

The folial pattern of the giraffe shows a marked difference in the anterior and posterior lobes. It also presents a well defined lobulus simplex. The anterior lobe

is relatively simple in its arrangement, the fissura primaria appearing cephalad to the midpoint of the folial pattern and presenting a rather wavy course outward and forward. The mesial extent of the anterior lobe is much greater than the lateral extent. The fissura secunda appears in the usual position between lobuli B and C and serves to mark off the extremely convoluted portion of lobulus C from the simple vermal pattern of lobulus B. It is continued outward and limits caudally the lobulus paramedianus. Lobulus 1 is a simple vermal lobulus. Lobulus 2 is divided on the surface into two subdivisions, the cephalic portion corresponding to the first two stalks and the caudal portion to the rather large third ray forming the major part of lobulus 2. The lateral extensions progressively increase in length. The folia show a definite vermal subdivision by short sulci which proceed outward for a variable distance. Lobulus 4 presents a distinctly triangular appearance and, together with the other lobuli of the anterior lobe, forms an almost perfect triangle. The cephalic folia forming lobulus 4 A are simply arranged and extend from the median line to the periphery. They are wide folia presenting short vermal sulci. The succeeding folia show a variable degree of lateral extent. The cephalic group begins with four separate folia and concludes as a single folium. The sulci extend for a variable distance into the hemisphere. There then succeeds a group of convergent, short folia, forming the median portion of this lobule, and then a single caudal folium which extends throughout the entire breadth of the anterior lobe. Lobulus C is subdivided into two very different portions. The cephalic division of lobulus C 2 presents a simple arrangement of vermal folia which continue outward as a series of long folia which, in general, are somewhat concave forward and tend to converge on the fissura primaria. These represent the emergence of the folia which were seen in the depths of the fissura primaria. There is a considerable reduplication of the folia forming the lateral portion of the lobulus. There is also a considerable number of vermal sulci. The caudal portion of lobulus C presents a high degree of vermal reduplication which has the peculiar characteristic of being limited almost entirely to the right half of the vermis. The lamellar chain presents three definite wide swinging extensions into a paravermian position, the mesial loops being continued over into the left side of the vermis and producing two small limited folial groups. The middle one of these three right lateral vermal loops shows a continuation outward into a folial rosette which interrupts the orderly course of the lobulus paramedianus. On the left side of the vermis a structure somewhat similar to this rosette appears, a series of folia which are continuous cephalically and caudally with the left lobulus paramedianus. The lateral portion of lobulus C 2 presents a lobulus ansiformis with a fairly well defined crus 1 and crus 2. Crus 2 is continuous caudally with a group of folia which is connected with the first of the right lateral vermal loops. It is then interrupted by the rosette which is projected outward from the paravermian region into the paramedian formation. The rosette is continuous by means of its peduncle with the cephalic portion of the second of the vermal loops. This rosette is then continued caudally as the remainder of the lobulus paramedianus, connected both directly and in the depths with the third lateral loop of vermal C 1.

Lobulus B consists of a series of folia which caudally presents slight lateral reduplication. These folia are gathered into a distinct peduncle parallel with the fissura secunda, passing to the base of the lobulus parafloccularis. The lobulus

parafoccularis is a direct continuation of the folial chain forming the lobulus paramedianus and arises as a short string of folia which is succeeded by a series of folial rosettes varying in size and complexity. This row of folial rosettes continues forward and outward along the lateral aspect of the lobulus paramedianus, crus 2 and crus 1, to the caudal limit of the lobulus simplex, where the chain of rosettes turns on itself outward and then backward to terminate in a rosette. Lobulus A consists of a series of vermal folia forming a rosette which sends its peduncle outward in the general direction of the lobulus floccularis. The lobulus floccularis is a direct continuation of the lobulus parafoccularis. It presents a single rosette and a terminal group of folia. It is situated in the usual position between the peduncle of the cerebellum and the parafoccular formation.

The implantation of the folia in the medullary substance shows that the first and second lobuli are inserted together. The fourth lobule has an implantation which becomes continuous with that of the lobulus simplex, the lobulus ansiformis and the lobulus paramedianus. The lobulus parafoccularis is based on a broad implantation into the medullary substance ventral and lateral to the main mass of the anterior and posterior lobes.

Physical characteristics of Giraffa camelopardalis

The giraffe is the tallest of all the mammals, reaching a height of 20 feet. The body is of moderate size; the legs are long, slender and powerful, the fore limbs being somewhat longer than the hind limbs and thus raising the body higher at the shoulder than at the rump. The neck is long and tapering, and is surmounted by a rather small head. The eyes are laterally placed but look considerably forward so that there is a definite overlapping of the visual fields. The movements of the eyes are conjugated and with an apparently considerable range of mobility. The ears are elongated, tapering and actively movable. The upper lip is moderately elongated and prehensile. The tongue is about 18 inches in length, is actively prehensile and is used to drag leaves, twigs and branches into the mouth. The neck is long and mobile, and the giraffe is extremely accurate and agile in the movements of the neck in going at full speed through trees and underbrush. The gait is that of a pacing horse; it is awkward in appearance but of about the same speed as that of a good horse. There is but little unilateral independence of the limbs. The tail is quite long but does not possess any special function.

BOS (CALF)

The arbor vitae of the calf is relatively extensive and presents a mass of subsidiary branching and foliation which is relatively more extensive than that found in other ungulate cerebella of the same size. The caudal extension of the medullary substance in the posterior lobe is typical of the ungulate group. The fissura primaria appears in the vertical position and is situated directly opposite the fastigial recess which is wide open, these two structures together dividing the arbor vitae of the cerebellum into the anterior and posterior lobes, the latter being considerably larger than the former. The fissura secunda appears in the usual position between lobuli B and C. It divides the posterior lobe into a much more extensive dorsal and a much less extensive ventral portion. The ventricular fastigium is

situated about the midpoint of the ventral portion of the cerebellum and is relatively wide open, but becomes reduced to the usual width as it approaches the medullary substance.

The medullary substance presents a U-shaped disposition, with a well marked condensation in the center of the anterior lobe, from which passes vertically a heavy ray 4, while there is a long drawn-out extension which proceeds upward and backward into lobulus C as the main core for the posterior lobe.

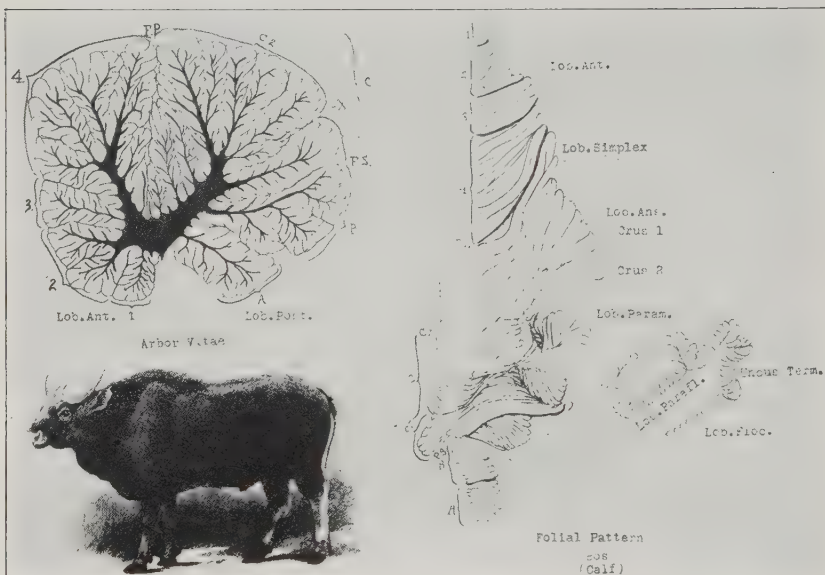


FIG. 11. *Bos* (calf)

The medullary rays

The first branch from the medullary substance, except a small inconsequential nubbin, is a slender stalk arising a short distance in front of the fastigial recess and giving off side branches. The medullary rays forming the second group consist of a single stout extension forward and downward which immediately subdivides into two subsidiary branches which again undergo considerable rapid division. Ray 3 appears at the junction of the second and fourth medullary rays with the anterior medullary substance. If the independence of this ray should be questioned, it undoubtedly should be assigned to lobulus 2, on account of the lamellar arrangement found in the folial pattern. It is a slender ray giving off side branches and dividing into two main subdivisions at its summit. Ray 4 is a heavy prolongation upward and forward of the medullary substance, is thick and gives off a number of small subsidiary branches before it divides into its termi-

nal group. The terminal group consists of three chief branches: a cephalic, which again divides into two well defined stalks; a dorsal, which presents side branches and a terminal division and a caudal, which is more slender and undergoes less extensive division. There then arises from the caudal aspect of the stem of ray 4 a series of twigs which are hidden in the depths of the fissura primaria. The posterior medullary substance is drawn out into a thick, heavy prolongation upward and backward, and presents on its concave dorsal surface a number of rather extensively divided stalks which arise in the depth of and from the caudal boundary of the fissura primaria. The end of ray C divides into two chief subdivisions: (1) a heavy dorsal stem, which again divides into three chief branches, that in turn subdivide to produce an extensive lobulus C 2, and (2) a direct caudal extension of the posterior medullary substance which is drawn out into a long slender ray C 1 that sends out many side branches and then divides at its summit into a spray of rays which support a series of relatively wide folia. In the depths of the fissure separating lobuli C 1 and C 2 is a twig which arises from the base of ray C 1 and is of importance on account of the fact that it represents a connection in the arbor of a group of folia which appear in the lateral folial chain between crus 2 and the paramedian formation. Ray B arises from the caudoventral aspect of the posterior medullary substance and presents a series of ventral branches of sufficient size to produce a series of sublobules on the ventral aspect of lobulus B. Ray A is a slender stem presenting side branches most of which undergo secondary division.

The lobules

Lobulus 1 forms the cephalic limit of the ventricular fastigium and is a relatively well developed lobulus. Lobulus 2 and lobulus 3 may be grouped together as the usual arrangement found in the ungulates, but on account of the fact that ray 3 has an entirely independent origin from the medullary substance, it is given an identity of its own. Lobulus 4 is relatively extensive, and forms the cephalodorsal angle of the anterior lobe and the cephalic boundary of the fissura primaria. It presents a grouping of folia which might warrant a division into lobuli 4 A and 4 B. On its caudal aspect it shows a number of compressed folia which extend only for a short distance laterally and can be seen in the folial pattern only if the fissura primaria is opened up. Lobulus C is divided into an extensive C 2 which presents an extensive degree of subdivision. There are a number of submerged folia in the depths of the fissura primaria which have only a limited participation in the folial pattern and are succeeded by an extensive group which appears on the surface and forms the chief mass of lobulus C 2. At the termination of lobulus C 2 in the depths of the fissure between it and lobulus C 1, there is a group of folia which is important on account of the fact that it connects laterally with the peduncle of a distinct roset which participates in the production of the paramedian formation. Lobulus C 1 is not extensive and presents on its surface only a small number of laminae. Lobulus B is relatively compressed at its origin but expands at the periphery into three groups of folia. The most dorsal group is rather irregular and may be divided into two subgroups which, in the folial pattern, are seen to be implicated in a transposition of the folial chain from one side to the other. The two other more caudal groups are simple and represent the serial arrangement

of two groups of folia. Lobulus A forms the caudal limit of the ventricular fastigium. It is a relatively simple lobulus, although it is of considerable size, and some of its branches are moderately subdivided.

The folial pattern of Bos

The folial pattern of the calf shows an arrangement similar to that seen in the other ungulates in its division into anterior and posterior lobes by the fissura primaria. The lines, however, are considerably straighter and less tortuous, and the folia are, in general, arranged in a more parallel manner. This may be due to the possible immaturity of the animal. The fissura primaria is situated somewhat in front of the midpoint of the folial pattern and extends out as a relatively simple straight sulcus toward the periphery. The anterior lobe is considerably less in extent than the posterior lobe, and the folia are arranged in a more regular fashion extending outward. There is less indication of a vermal portion, the vermal sulci being less pronounced and showing but little tendency to form a paramedian furrow. The fissura secunda appears as usual between lobuli B and C and is connected with the termination of the paramedian formation. Lobulus 1 consists of a group of vermal folia which shows some convergence, being implanted by means of a single peduncle. Lobulus 2 is divided into two portions—a cephalic vermal, and a caudal division. If lobulus 3 is grouped with lobulus 2, this differentiation between the cephalic and caudal portions of the combined lobules becomes more marked. Lobuli 2 and 3 are implanted by a more or less common peduncle into the medullary substance. Lobulus 4 is fairly extensive in the vermis but much reduced in the hemisphere owing to the fact that many of the folia fail to reach the periphery, six chief folia being reduced to three. At its caudal portion is the group of folia in the depths of the fissura primaria which has been noted in the arbor vitae. Lobulus C is divided into a much more extensive cephalic portion, lobulus C 2, and a much reduced caudal portion lobulus C 1. The cephalic portion is again subdivided. The cephalic part consists of a fairly regular group of lamellae, the lobulus simplex, which runs toward the periphery, bending forward and being reduced in size as it approaches the periphery of the hemisphere. There is a definite division into vermal and lateral portions, with the indication of a paramedian furrow. The caudal vermal portion of the cephalic subdivision of lobulus C 2 shows the beginning of a loop, the folia being arranged chiefly on the right side of the vermis. As the folial chain is followed, a swing over to the left side of the vermis occurs. The folia of the caudal vermal portion of lobulus C 2 then are succeeded by the lamellar chain of lobulus C 1 which is wide and crosses the midline with the loop first on the left side and then on the right side of the midline. These folia are continued out on either side to become directly continuous with the most caudal of the paramedian folia. The hemispherical portion of lobulus C presents the usual fairly simple arrangement in the cephalic portion corresponding with the lobulus simplex. As these lamellae shorten, crus 1 of the ansiform formation appears and rapidly extends outward with shortening folia, forms its apex and then turns back and inward as crus 2, producing a distinct intercrural sulcus with a number of simple folia interposed between the caudal extremity of crus 2 and the succeeding folia, which form a rosette and are connected with the submerged

group of folia in the sulcus between lobulus C 2 and lobulus C 1. This twists outward with the formation of a cluster of folia and ushers in the paramedian formation, a characteristic interpolation between crus 2 and the lobulus paramedianus of the ungulates. The paramedian formation then appears as a series of wide folia which proceed caudally and then form a caudal elbow, the folia rapidly diminishing in width to become continuous with a series of wide vermal folia representing lobulus C 1. Lobulus C 1 presents an extensive lateral disposition, the vermal folia being directly continuous with the lateral folia forming the caudal termination of the lobulus paramedianus as it approaches the lobulus parafoccularis. Lobulus B shows a rather thick twist of considerable extent, the folia converging in a large cluster formation which is situated to the right of the midline. The rest of lobulus B lies in the midline, although more to the left. A peduncle forms from the two parts of lobulus B which can be traced outward in the direction of lobulus parafoccularis. The lobulus parafoccularis begins as a series of folia directly continuous with the folia forming the lateral extension of lobulus C 1. This group continues outward forming a series of loose clusters not nearly so extensive as those of *Camelus*. The parafocculus continues forward around crus 1 turning inward completely to surround crus 1, then turns backward and outward, and then inward again to terminate in a distinct uncus terminalis along the under surface of the first portion of the lobulus parafoccularis. Lobulus A consists of a simple group of folia arising from a single peduncle which may be traced outward a short distance but loses itself in the medullary substance, but in the general direction of the lobulus floccularis. The lobulus floccularis consists of a simple cluster of folia in those relationship with the termination of the uncus terminalis succeeded by a diminishing chain of lamellae which continues inward toward the vermal portion of the cerebellum. The lobulus floccularis occupies its usual position between the peduncle of the cerebellum and the parafoccular formation.

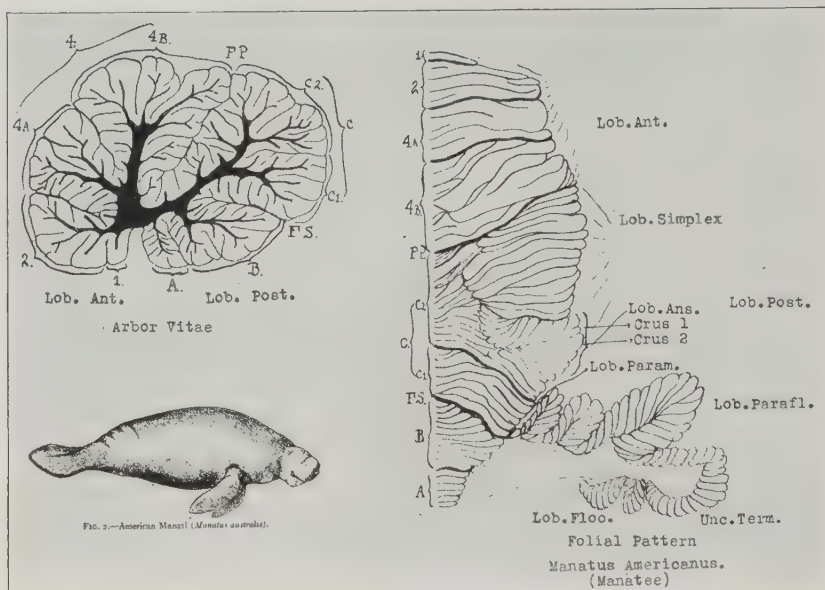
The main mass of the posterior lobe is inserted in the medullary substance by means of a broad attachment supporting the lobuli simplex, ansiformis and paramedianus, while the lobulus parafoccularis finds an attachment to the medullary substance which is in the usual position lateral and ventral to the mass formed by the ansiform and paramedian formations.

Physical characteristics of Bos taurus

The cow is a relatively heavy bodied ungulate. The legs are rather short, the fore limbs being somewhat shorter than the hind limbs, so that the animal slopes somewhat from his rump to his shoulder. The neck is short and thick. The head is heavy. The eyes are placed in the lateral surface of the head but have a considerable overlap in the visual fields. They are possessed of conjugate movement. The lips are somewhat prehensile. The tongue is thick and is actively mobile. The neck is possessed of a fair range of movement. The limbs are almost entirely for the purpose of locomotion, and possess but little unilateral independence. The tail is long and is used only to keep the animal free from flies. The cow is not possessed of much speed, and is rather slow and awkward in its movements.

MANATUS AMERICANUS (MANATEE)

The arbor vitae of the manatee is distinctly oval in outline, the horizontal being greater than the vertical diameter. It is much simpler than the ungulate cerebellum, the pattern being relatively coarse, with only a small degree of foliation. It is divided into approximately equal anterior and posterior lobes by means of the fissura primaria and the ventricular fastigium. The fissura primaria is situated behind the middle of the arbor vitae and proceeds forward and downward toward the fastigium. The fissura secunda appears in its usual position between lobuli B and C. It is situated somewhat above the level of the medullary substance

FIG. 12. *Manatus americanus* (manatee)

and proceeds backward and slightly downward, dividing the posterior lobe into a much larger dorsal and a much smaller ventral portion. The medullary substance is disposed in a rather irregular manner. It presents a large mass in the center of the anterior lobe with a heavy extension upward forming ray 4. The medullary substance presents a constriction at the point where the fissura primaria approaches the fastigium, and is continued into the posterior lobe as a long caudal stalk which is continuous with ray C.

The medullary rays

Ray 1 is a slender, undivided branch from the ventral aspect of the anterior medullary substance. Ray 2 arises as a simple direct extension forward of the

medullary substance, giving off lateral branches. Ray 4 arises as a heavy upward prolongation of the entire medullary mass. It gives off a heavy stalk cephalically, ray 4 A, which gives off lateral branches and subdivides. The continuation of ray 4 proceeds upward as a thick, heavy stalk, ray 4 B, giving off rather simple side branches, and then divides into three terminal branches, the first of which proceeds forward and forms a simple folial cluster, the second upward with a restricted division and the third backward. Ray C arises as a direct caudal prolongation of the posterior medullary substance, proceeding backward and upward, and divides into ray C 1 and ray C 2. Ray C 2 continues upward in a rather concave direction, and divides into a vertical and a horizontal division, the latter being somewhat more extensive than the former. Ray C 1 proceeds directly backward, giving off lateral twigs, and subdivides into two terminal branches. Ray B arises from the under surface of the caudal continuation of the posterior medullary substance, as a thick branch which divides into a caudal horizontal branch which gives rise to a number of secondary twigs and a ventral stem which is quite short. Ray A appears as a slender stem from the under surface of the posterior medullary substance, giving off lateral branches.

The lobules

Lobulus 1 appears as a single folium forming the cephalic margin of the fastigium. Lobulus 2 appears as a simple lobulus made up of rather coarse folia. Lobulus 4 is divided into two lobules, lobulus 4 A and lobulus 4 B. Lobulus 4 A forms the cephalic subdivision of lobulus 4 and consists of a few coarse folia. Lobulus 4 B is much more extensive and forms the summit of the anterior lobe. It is made up of a number of coarse folia, which may be rather irregularly arranged into three sets of folia. Lobulus C is divided into lobulus C 2 and lobulus C 1. Lobulus C 2 forms the caudal boundary of the fissura primaria. It is not extensive and is made up of a number of coarse folia, the caudal folia being slightly more numerous. Lobulus C 1 is a simple lobule, forming the caudal portion of lobulus C. Lobulus B is a rather large lobule made up of coarse folia distinctly subdivided into two portions. Lobulus A is a simple lobulus forming the caudal margin of the fastigium.

The folial pattern of Manatus americanus

In general, the folial pattern is relatively simple. The folia pursue a fairly regular lateral direction. All the fissures and sulci are more or less parallel except in the caudal portion of lobulus C 2. There is no marked expansion laterally of the folial pattern at any point, the periphery of the folia showing a more regular outline than that found in any cerebellum except that of *Bradypus tridactylus*. The fissura primaria appears at about the middle of the arbor and proceeds almost directly outward with only a slight inclination forward. The fissura secunda appears in its usual position between lobuli B and C. It proceeds outward and somewhat backward, forming the apparent limitation between the paramedian formation and lobulus parafloccularis. Lobulus 1 consists of a single vermal folium. Lobulus 2 consists of three folia presenting a few vermal sulci and a single independent lateral sulcus dividing the middle folium. The folia of lobulus 2 are continued into a definite lateral portion. Lobulus 4 A consists of a wide cephalic

folium subdivided mesially by vermal sulci and partially divided at the periphery. The caudal folium of lobulus 4 A presents a vermal sulcus with a tapering lateral extension. Lobulus 4 B presents a number of cephalic folia which converge on the sulcus separating lobulus 4 A from lobulus 4 B. Succeeding this is a relatively wide folium, proceeding forward and outward reaching the periphery. The succeeding folia are irregular and show vermal divisions and lateral portions. The sulci seems to show a tendency to wander aimlessly across the folia, many of them joining together. A considerable degree of reduplication appears in the most caudal folium at the periphery. Lobulus C is divided into two portions, lobulus C 2 and lobulus C 1. Lobulus C 2 presents a distinct differentiation into vermal and lateral portions. The vermal folia are narrow, irregular and tend to run forward converging on the fissura primaria. In the middle of lobulus C 2, they become somewhat more regular and are apparently continuous with the lateral chain of folia. In the caudal portion of the vermis, the folia of lobulus C 2 have a regular arrangement and are continued outward and backward into a peduncle which joins the caudal portion of the lateral folial chain. The lateral folial chain presents a simple arrangement of serial folia in the cephalic portion of lobulus C 2. This may represent an indefinite lobulus simplex. The chain continues backward as a series of relatively wide folia, and in its caudal third presents a distinct roset which may be recognized as the lobulus ansiformis, with a crus 1 and a crus 2 forming the sulcus intercruralis. Lobulus C 1 presents in its cephalic portion a number of vermal folia which run forward into the sulcus between lobulus C 1 and lobulus C 2. The caudal folia of lobulus C 1 arrange themselves in more or less parallel strips, running outward and backward, and are continuous with the folia of the lateral chain which now appear as undivided strips extending from the midline to the periphery. The folia at the periphery represent the lobulus paramedianus. Lobulus B appears as a group of folia increasing in width to an apex and then diminishing in a regular series. These folia produce a rosette, the peduncle of which proceeds outward and is apparently continuous with the base of the lobulus parafoccularis. The lobulus parafoccularis appears as a continuation of the folial chain of the lobulus paramedianus, into the parafoccular formation. The parafocculus appears as a series of folial rosettes, small at the beginning and becoming much larger, applied to the lateral surface of the lobulus paramedianus and the lobulus ansiformis as far forward as the fissura primaria, then returning in a rather irregular series of rosettes and loops forming a definite uncus terminalis. Lobulus A presents a simple series of diminishing vermal folia, connected by means of a peduncle with the lobulus floccularis. The lobulus floccularis appears as a continuation of the lobulus parafoccularis, beginning as a rosette, and then showing an increasing and next a diminishing folial chain. It is situated between the peduncle of the cerebellum and the parafoccular formation.

The lobules and the folia are implanted in a rather simple manner into the medullary substance. The lobules of the anterior lobe tend to converge on a single broad implantation into the medullary substance, while a similar course is followed by the lobulus of the posterior lobe. The parafoccular formation is inserted by means of a broad base into the medullary substance, lateral and ventral to the rest of the posterior lobe.

Physical characteristics of Manatus americanus

The manatee represents *Sirenia*. Its present degenerated physical condition is due to its specialized adaptation to an aquatic habitat and a herbivorous diet. The body, about 8 feet in length, is essentially fishlike, the neck having gradually shortened and externally disappeared. The eyes are small, with imperfect eyelids and a nictitating membrane. The lips are extraordinarily modified, the upper lip being divided by a wide groove into two mobile, swollen pads which are prehensile and, without the aid of the lower lips, can draw food into the mouths. The fore flipper is oval; it is capable of free movement at the shoulder, elbow and wrist joints and bears three vestigial finger-nails near the tip. The tail is flattened, sharply rounded off behind and not notched. The hind limbs have completely disappeared externally.

PHOCAENA COMMUNIS (PORPOISE)

The arbor vitae of the aquatic mammals belonging to the cetacean group offer extreme difficulties in a determination of the identity of the various lobes, lobules, and fissures. From the form of the arbor vitae and the general distribution of the branches of the medullary rays, it is impossible to determine the exact position of the various fissures, and, therefore, the task of dividing the arbor vitae into the various lobules is almost impossible. A careful study of the arbor vitae, together with its connections with the folial pattern, indicates certain relationships which make it possible tentatively to divide the arbor vitae according to the scheme which has already been followed. The arbor vitae of *Phocaena* can be analyzed by first establishing the connections of the flocculus, paraflocculus and what would correspond with the lateral extension of lobulus C. According to this method, the posterior lobe apparently consists of a peculiar, distorted folial growth which appears collected in the caudal portion of the arbor vitae and consists of two peculiar medullary rays which are practically devoid of cortical covering, but are found to be continuous with an enormous expansion in the hemisphere and seem to combine the lobulus ansiformis and the lobulus paramedianus. If this demarcation is correct, the remainder of the foliated rays belong to the anterior lobe. The further allocation of the anterior rays into the lobules indicated appears to be warranted by a study of the connections of the foliated portions of the hemisphere with the various lobules of the arbor vitae. The arbor vitae itself does not supply any definite idea as to the identity of the various rays and lobules. Assuming that this arrangement is correct, which is not at all firmly established, the fissura primaria appears to be a small fissure separating the large medullary rays which form a corona around the ventral, cephalic and dorsal surfaces of the arbor vitae from a series of peculiar structures which have but little representation in the arbor vitae, but have an enormous expansion in the hemispheres. The ventricular fastigium is the only structure which can be definitely recognized, and it appears on the ventral surface of the arbor vitae, lying almost at the caudal extremity, and is succeeded by only two rudimentary folial groups which represent lobulus A and lobulus B 1 of the larger lobulus B. The fissura secunda lying, as it should, in front of the arbor lobule connected with the paraflocculus is determined as the ill defined fissure lying between the second of the peculiar rays of lobulus C and the

equally peculiar terminal tail-like outgrowth from the medullary substance which forms ray B 2, the chief connecting link with the lobulus paramedianus and the parafocculus. The determination of the fissura primaria divides the arbor vitae into an enormous expansion comprising almost the entire surface of the arbor vitae as the anterior lobe, and a small, peculiarly arranged group of rays with only a minimum of folial representation as the posterior lobe. With this as a basis, the lobules and rays of the anterior lobe may be subdivided in a relatively satisfactory manner. The medullary substance of the arbor vitae of *Phocaena* presents a

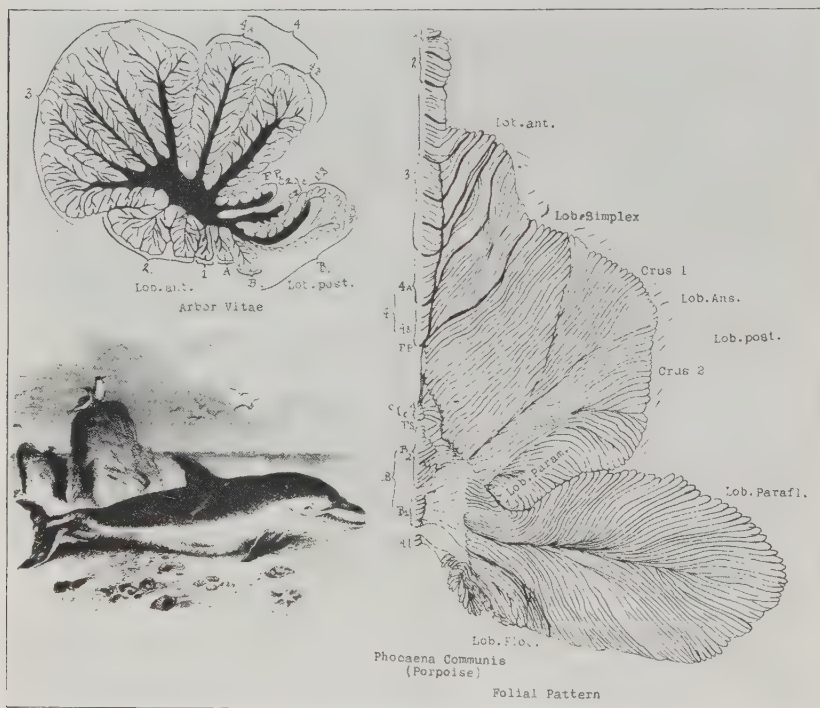


FIG. 13. *Phocaena communis* (porpoise)

rather remarkable appearance. It consists of a relatively large mass of white matter which is almost completely disposed in the anterior lobe, with only a small caudal extension into the posterior lobe. The anterior medullary substance is roughly quadrangular and appears in an oblique plane directed from behind forward and upward. From its cephalic extremity protrudes a heavy extension forward from which arises a fan-shaped group of medullary rays. At the point where the fissura primaria (?) approaches the ventricular fastigium the medullary substance suddenly undergoes a marked reduction and gives off the medullary rays which form

lobulus C, the small ray A and the rays which form lobulus B. The medullary substance is drawn out into a curved tail-like extension which forms the core of the chief portion of lobulus B.

The medullary rays

Ray 1 appears as a slender stalk proceeding directly downward, giving off a few lateral branches. The next two medullary rays arising independently from the ventral surface of the anterior medullary substance, the first being small and the second more subdivided, may apparently be grouped together as ray 2. The next group of rays comprises the major portion of the arbor vitae and presents itself as a group of five stalks arising from the enormous anterior extension of the medullary substance. The first of these is a thick, heavy stalk advancing directly forward and undergoing secondary division into two of the peculiar elongated frondlike developments which are characteristic of the arbor vitae of *Phocaena*. Following this, there are three long slender extensions from the medullary substance which appears as the leaves of a fan. These slender prolongations are richly supplied with lateral branches many of which undergo secondary subdivision. The last one is the most extensive in lateral width and presents a division at its summit into two major portions. The next two rays, ray 4 A and ray 4 B, arise from the dorsal surface of the medullary substance as two typical long drawn out frondlike groups of folia which present in their center a relatively thick medullary ray giving off numerous lateral side branches the majority of which are divided at their extremities. Ray C is divided into a U-shaped structure which arises from the posterior medullary substance, the cephalic branch from the caudodorsal angle of the medullary substance and the caudal branch from the tail-like extension of the medullary substance, and proceeds almost directly backward, presenting cortical tissue practically only on their unopposed surfaces. Lobulus B presents a structure which is somewhat reminiscent of the twisted lobulus C of the ungulate, being markedly convex with its ventral aspect practically bare of cortical tissue, while its dorsal surface presents a number of rudimentary branches forming definite folia. The peculiar arrangement of the folia as they leave this bare caudal surface is indicated by the folia which begin at once to draw away from the midline into the hemisphere. Ray B 1 appears as a small slender outgrowth at the base of ray B 2, presenting a few lateral branches. Ray A is an insignificant stem arising from the ventral surface of the posterior medullary substance.

The lobules

The various lobules based on this tentative identification of the medullary rays present a peculiar and unfamiliar appearance. Lobulus 1 appears as an insignificant group of folia forming the cephalic wall of the ventricular fastigium. Lobulus 2 appears to be composed of two folial groups developed on two independently arising medullary branches. The first stalk is relatively simple, being somewhat more developed than lobulus 1. The second stem is somewhat larger, and it undergoes a definite expansion as the ray leaves the medullary substance. At its summit it is divided into two groups of lamellae. Both of the rays forming

lobulus 2 arise from the ventral aspect of the medullary substance. The next group of rays may be combined together to form lobulus 3. This lobulus is complicated and is made up of four groups of folia, the first being the largest and being subdivided into two subsidiary portions. The two succeeding sublobules form narrow frondlike folial groups, while the most caudal is distinctly caudal in form, its apex being directed toward the medullary substance and the base at the periphery. This group of sublobules forms a large triangular mass making up the major part of the anterior lobe. Lobulus 4 appears to be made up of two folial groups which are independent of each other, and relatively richly foliated. Lobulus C is subdivided into two rudimentary arbor divisions presenting cortical tissue only on the nonopposed surfaces of the U-shaped medullary extensions. Lobulus B has a minor representation in the arbor, but expands immediately on leaving the midline into the enormous parafoccular formation and is subdivided into lobulus B 2 and lobulus B 1. Lobulus B 2 is scimitar-shaped, the dorsal aspect being subdivided into a large number of folia, and the ventral aspect being formed chiefly by the medullary ray with a film of almost undifferentiated cortical tissue covering it. This in the folial pattern is seen to be a peduncular formation which expands into the enormous folial pattern of the parafocculus. Lobulus B 1 is a simple, poorly differentiated lobulus. Lobulus A is a simple folial group.

The folial pattern of Phocaena communis

The folial pattern of the dolphin presents a peculiar appearance owing to the fact that the parafocculus forms fully a third of the entire substance of the hemisphere. The lateral expansion of lobulus B forms the greater part of the posterior lobe, the entire anterior lobe representing only a negligible contribution to the hemisphere. If the identification of the fissura primaria is accepted as correct, the fissure appears at almost the most caudal part of the vermal folial pattern. The entire vermal extent of the posterior lobe corresponds to about one-fifth of that belonging to the anterior lobe. The fissura secunda appears as a definite line of demarcation between the lobulus paramedianus and the parafoccular formation. The folial pattern of the anterior lobe shows an absolutely definite division into vermal and lateral portions. Lobules 1 and 2, and the cephalic third of lobulus 3, do not present any lateral extension, the folia being confined entirely to the vermal midline, presenting a few medial subdivisions. Lobulus 1 presents only two small vermal folia while lobulus 2 consists of five or six folia. The middle and caudal thirds of lobulus 3 present definite lateral extensions. The caudal half of lobulus 3 presents a definite paravermian sulcus into which the folial sulci descend, and only with considerable difficulty can the proper continuation of each folium into the hemisphere be identified. The lateral extensions of the caudal folia of lobulus 3 present a few vermal folia which extend into the paravermian groove and then pass on to the periphery. The lateral extensions are not so numerous, as the vermal folia turn forward at quite an angle. Lobulus 4 consists of two groups of folia corresponding to the two medullary rays. These vermal folia are strongly limited by the paravermian groove, the folia continuing outward; those belonging to 4 A present the emergence of a number of submerged folia from the depths of the fissure separating lobulus 3 from lobulus 4. Lobulus 4 B consists of a series of

slender folia continuing outward to the periphery and beginning to present the appearance of the folia forming the lateral expansions of lobulus C. Lobulus C presents an almost rudimentary folial development of two groups of only two vermal folia each. These folia, however, are supplied with a strong peduncle which diverges markedly from the base of the medullary rays and immediately expands into an enormous structure composed of a series of lamella arranged in a more or less definite form as a lobulus simplex, consisting of narrow strip-like parallel folia that are marked off from the succeeding folia which establish the ansiform formation with its crus 1 and crus 2. Crus 1 and crus 2 appear as two groups of converging fanlike folia the mesial extremities of which form an intercrural sulcus. Then there succeeds a series of folia which gradually diminishes in extent and concludes as a group of submerged folia joining the folia of the parafloccular formation. This group of folia corresponds to the paramedian formation. Lobulus B presents two definite groups of folia. A caudal group, lobulus B 1, consists of six or seven folia; these are connected by a strong bare medullary peduncle with the enormous parafloccular formation. The remainder, lobulus B 2, presents a definite arbor structure which expands into a lateral extension connected with the caudal portion of the large lobulus representing the ansiform and paramedian formations. The major portion of lobulus B 2 is connected with the curled under folia forming the lobulus paramedianus. The parafloccular formation appears as a series of long slender folia which extend outward into an enormous structure, gradually coming to an apex and returning on itself, and thus forming a definite interparafloccular sulcus. This enormous parafloccular formation is turned underneath the projecting mass of what corresponds to the ansiform formation. It forms the ventral third of the entire cerebellar mass. Lobulus A consists of only two folia which are connected by means of a narrow peduncle with the lobulus parafloccularis which occupies an excavated corner in the mesial and caudal aspects of the lobulus parafloccularis. These folia form a series of extended rosetts, diminishing progressively as the median line is approached.

Lobulus 1 and lobulus 2 show a common peduncular insertion into the medullary substance. Lobulus 3 has two peduncles, one for the cephalic third, the other for the caudal two-thirds. Lobulus 4 has a separate peduncle. Lobulus C has a simple broad implantation, while the paraflocculus constituting the major portion of the posterior lobe is implanted laterally and ventrally to lobulus C.

Physical characteristics of Phocaena communis

The dolphin is a representative of the much altered aquatic mammals who have acquired an extensive adaptation to a new environment. The aquatic mode of life in connection with the retention of the needs connected with their type of dietary has resulted in an active, wide range type of animal capable of great speed and agility. The dolphin attains usually a length of from 8 to 10 feet. The body is fishlike and does not show any external differentiation between the head and the body. The eyes are small and laterally placed, and have no overlap in the visual fields. The eyes are incapable of movement and are of use only under water and at close range. The jaws can be opened to a moderate extent. The tongue is short and is not protrudable. The fore extremities are reduced to a pair of fins

which are used in swimming and possess but little unilateral independence. The hind limbs have been entirely suppressed, as far as their surface representation is concerned. The tail is broad, horizontally fluked and powerful. The dolphin is capable of considerable speed, can leap for some distance out of the water and is possessed of great agility in its pursuit of food and its contacts with friends and enemies.

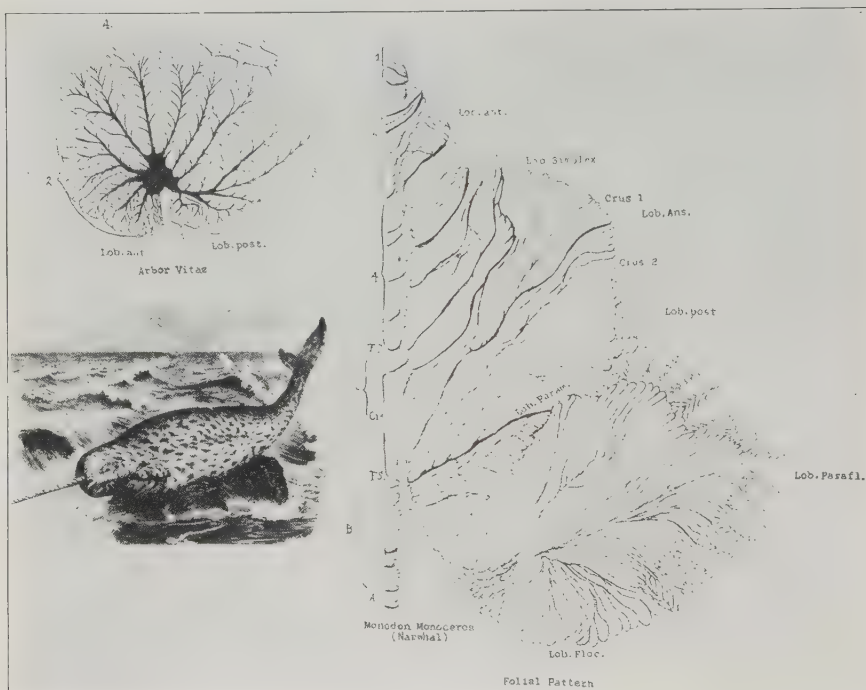


FIG. 14. *Monodon monoceros* (narwhal)

MONODON MONOCEROS (NARWHAL)

The identification of the various fissures and, therefore, of the lobes and lobules of the arbor vitae presents the same difficulties which were experienced with *Phocaena*. The identification of the ventricular fastigium is easy, quite a gap appearing between the lobules of the anterior and posterior lobes. A number of fissures, however, would qualify as the fissura primaria, especially one which approaches somewhat from behind and which appears in about the same position as that determined for the fissura primaria in *Phocaena*. A combined study, however, of the arbor vitae and the folial pattern seems to indicate that this is rather the fissura secunda, and that the fissura primaria lies in front of the two

rays which precede the fissura secunda. The fissura primaria, therefore, proceed from above downward and somewhat forward, and approaches the fastigium almost at its apex. With these surface markings identified, the anterior lobe is shown to be considerably larger in extent than the posterior lobe.

The medullary substance consists of a large cephalic condensation from which arise the various rays, subdividing the lobe into its lobules. The posterior medullary substance is much smaller, and consists of a tapering protrusion of medullary substance into the posterior lobe, from which dorsally arises ray C, and from its caudal extension, rays A and B.

The medullary rays

Ray 1 appears to be incorporated with the superior medullary velum as a well defined lingula. The medullary rays forming lobulus 2 arise as a group of three independent stalks the first of which is slender and gives off only lateral branches; the second is heavier and, in addition to lateral branches, presents a terminal division, while the third is still heavier and possesses the same sort of division. These independent stalks are then followed by a heavy cephalic extension of the medullary substance which gives rise to two primary divisions; the first gives off only small lateral twigs while the other gives off extensive cephalic branches. Ray 4 takes origin by means of a thick, heavy extension upward of the medullary substance. It gives rise at its summit to three diverging stalks, all of which are richly subdivided and terminate in bushlike folial collections. The rays for lobulus C arise as two independent slender extensions of the medullary substance which gives off a great number of lateral subdivisions. Ray B arises as a direct extension backward of the medullary substance, giving rise to a thick ventral branch, which is not extensively subdivided, and a dorsal branch, which divides into three slender stalks, the middle one being the most extensive. Ray A is an angulated, slender ray which arises from the root of ray B.

The lobules

Lobulus 1 consists of a lingula presenting three or four folia. Lobulus 2 consists of three sublobules provided with independent medullary rays, and a consolidated lobulus consisting of about five sublobules, formed by the bifurcation and further division of the most dorsal of the rays entering into the formation of lobulus 2. Lobulus 4 consists of three chief sublobules, each of which is subdivided. All these lobules are somewhat pyriform, the base being at the periphery, and they decrease in size from before backward. They consist of elongated folial groups which, at the periphery, fan out into rather extensive lamellar clusters. They are quite deep. Lobulus C consists of two groups of folia produced by the formation of two medullary rays, and are similar to the sublobules of lobulus 4 but are less extensive. Lobulus B consists of four chief subdivisions, the dorsal two of which are long slender prolongations from the upper medullary ray, succeeded by a short, ill defined sublobulus, and then by a larger terminal ventral lobulus. Lobulus A consists of a group of simple folia, partially overhung by the caudal termination of lobulus B.

The folial pattern of Monodon monoceros

The narwhal presents a degree of complexity unequaled by any folial pattern which has been examined. The lateral hemisphere of the elephant exceeds it in bulk, but is much more easily divisible into the main components of the hemisphere than are the folia of the narwhal. The chief difficulty in the division of the hemisphere into its constituent lobules is the fact that there is apparently no definite relationship between the hemispherical lobules and the lobules of the arbor vitae, the major subdivisions of the folial grouping apparently falling midway between the divisions of the arbor vitae, so that each one of the folial extensions belongs half to the preceding and half to the succeeding arboreal division. A similar difficulty arises in the division of the lobules at the periphery, since here also there is no clear differentiation between the folial groups, each succeeding group being connected with the preceding folial group, usually in the depths of the fissura separating them, by a large mass of connecting and communistic folia.

The fissura primaria, identified as well as possible, begins at about the middle of the arbor, but proceeds sharply forward so that it divides the folial pattern into an almost inconsequential anterior lobe and an enormous posterior lobe. The fissura primaria passes outward and then forward in a rather irregular, sinuous line to the periphery. The fissura secunda appears between what may be identified as lobuli B and C. It cannot be identified with any degree of assurance in the hemisphere on account of the fact that it is difficult to determine where the lobulus parafloccularis begins. A well defined fissure exists between the main mass of what may be considered the lobulus ansiformis and the enormous extension of the parafloccular formation. The group of folia, however, interposed between this fissure and the main mass of the paraflocculus, presents such a striking resemblance to the paramedian formation that it is difficult to decide whether the fissura secunda lies in front of, or caudal to, this structure.

The anterior lobe shows a definite division into a vermal and a lateral position, there being a deep, narrow paravermian groove separating the vermal and the lateral folia. Into this groove the sulci separating the vermal folia pass, and then run forward for a considerable distance before passing outward into the lateral extensions. The exact correspondence of the lateral extension with the proper group of vermal folia is extremely difficult to determine. Lobulus 1 appears as a lingula, and presents four or five well defined folia which caudally become somewhat more elongated, but without forming any definite lateral extension. This group of folia forming lobulus 2 consists of four well defined groups. The first group consists of two or three small folia similar to those of lobulus 1. The second cluster of folia are drawn outward to an apex. The third portion consists of a single partially subdivided folium which is applied to the lateral aspect of the preceding group. The fourth portion consists of an initial folium which extends outward to participate in the apex formed by the two preceding groups of folia; the remaining lamellae are rapidly reduced to vermal folia of meager dimensions, the caudal of which are connected in the depths of the paravermian fissure with a peculiar extension into the lateral hemisphere, and the distal folia of which are placed at right angles to the usual direction of the hemispherical folia. Lobulus 4 consists of four well defined groups of vermal folia bounded by the deep paraver-

mian fissure through which the folial sulci proceed to become continuous with those separating the folia of the hemisphere. The folial extension of lobulus 4 consists of an extremely irregular series of folial groupings not presenting any definite characteristics but rather an extreme degree of variability and variety in the conformation, direction and arrangement of the folia. The folia, however, become progressively longer, as the chain is followed caudally, showing a constant tendency to diminish in number as the periphery is approached, so that the lateral extent of this group of folia is considerably less than its mesial representation. Lobulus C consists of two separate, distinct groups, a cephalic vermal lobulus C 2 consisting of two simple folia connected with an irregular lobulus that does not reach the periphery. This lobulus, from its location and vermal connections, should represent the lobulus simplex. The vermal folia of lobulus C 1 appear as two groups of folia which converge in the paramedian sulcus, becoming more and more oblique and less and less extensive. Connected with these two groups of vermal folia there is found an extremely irregular arrangement of hemispherical folia forming an irregular pattern of succeeding folial groups presenting the suggestion of an ansiform formation, a poorly developed crus 1 and crus 2, with the production of an intercrural sulcus. The folia of crus 2 and the paramedian formation present a series of rosettes at the periphery which afford the implantation into the medullary substance. Lobulus B presents four definite subdivisions in the folial collection: (1) a submerged group of six folia, (2) a group of twelve or fourteen folia which represent the long extension backward of the middle ray of lobulus B, (3) a few submerged folia representing the small folium between the dorsal and ventral branches of lobulus B and (4) a simple folial group, the ventral branch of lobulus B. These folial groups are continued outward by means of a heavy, dense peduncle with the caudal half of the ansiform formation or a large paramedian formation. The paraflocculus consists of an S-shaped curve of folial strips, beginning with a structure which presents a large but subordinate rosette formation with two definite crura and a series of rosettes in its second portion. After this a long series of folia appears which extend outward and at their lateral extremities present the peculiar implantation found in *Phoca*, a series of elongated folial rosetts formed on a peduncle which is inserted into the medullary substance and at its summit gives origin to at least two of the parafloccular folia. These are arranged as a fringe around the entire extremity of the paraflocculus. The rest of the folia of the paraflocculus are arranged in a series of elongated folia which converge at various points on each other, forming at least two interparafloccular sulci. The caudomesial angle of the parafloccular formation is excavated to receive the lobulus floccularis, consisting of a series of converging, rather broad folia, terminating in an elongated double roset. The base of the flocculus is somewhat covered by the base of the parafloccular formation itself, and is apparently continuous with a peduncle that develops at the base of the folial rosette which forms lobulus A.

The implantation of the various lobules into the medullary substance is relatively simple. Lobulus 1 and the major portion of lobulus 2 are implanted together. The lobulus simplex and the lobulus ansiformis share a rather wide peduncle. The lobulus paramedianus presents the peculiar rosette-like peduncles which develop as a fringe along this part of the cerebellum. The paraflocculus also possesses the same sort of an implantation, the rosettes being closely packed and succeeding one another without any appreciable interval.

Physical characteristics of Monodon Monoceros

Cetacea represent a group of mammals derived from a stock which also gave rise to *Carnivora*. *Cetacea* are carnivorous and their specialization has resulted from an early adoption of an aquatic habitat and a carnivorous dietary which made *Cetacea* a roving type of aquatic mammal. Like *Sirenia*, its aquatic habitat has rendered *Cetacea* essentially fishlike in form. The narwhal presents an elongated, tapering outline, the head and body being externally continuous and not presenting any cervical differentiation. It is usually from 12 to 15 feet long. The eyes are small and situated laterally. The visual fields do not overlap, and the eyes are immobile. The tongue is small. Protruding from the upper jaw is a twisted spear, which is usually single, although it may be double. The forelimbs are transformed into flippers which externally do not show any joints; the hind limbs do not show any external development. A dorsal fin is not present. The tail is formed of thickened integument and is provided with two heavy flukes situated in a horizontal plane. The narwhal proceeds through the water by swimming movements of the body and tail. It is capable of great speed and can maneuver with the greatest facility, grace and agility.

FELIS DOMESTICA (CAT)

The arbor vitae of the cat in median section presents a somewhat oval outline. The fissura primaria is almost vertical in position, situated a little in front of the midpoint of the cerebellum and almost directly opposite the approach of the ventricular fastigium to the medullary substance. The ventricular fastigium is almost perpendicular. The fissura secunda appears in the usual position, separating lobuli C and B. There is some disparity in the division into anterior and posterior lobes, the posterior lobe occupying a little more than half of the mesial surface. The medullary substance is relatively concentrated as a protuberant mass in the anterior lobe, the posterior lobe receiving a caudal extension of the medullary substance of the anterior lobe directed mainly upward into lobulus C.

The medullary rays

Ray 1 is a single branch arising from the ventral surface of the medullary substance of the anterior lobe, presenting a few lateral offshoots. Ray 2 consists of a rather massive extension forward of the main mass of the medullary substance and gives rise to three independent medullary branches which show a slight consecutive increase in complexity. Ray 3 arises at the junction of the root of ray 4 with the main mass of the medullary substance and may be recognized as an independent branch. It is a simple, slender ray, giving off side branches, and ends in a secondary subdivision. Ray 4 is a somewhat heavier stem arising almost perpendicularly from the dorsal surface of the medullary substance and dividing into two main branches which again undergo a single division. Ray C, subdivided into ray C 2 and ray C 1, represents the chief caudal extension of the medullary substance of the posterior lobe, being directed upward and backward as a relatively thick stem, ray C 2 giving off simple branches from its cephalic and caudal aspects, and then undergoing an extensive terminal division. The cephalic group of

terminal branches supports transverse folia, while the caudal branches participate in the formation of a loop in the vermis. In the depths of the fissure between rays C 1 and C 2 are found two branches which, when followed into the folial pattern, form the basis for the twisting turn of the vermal folia. Ray C 1 arises as a single independent shoot close to the junction of C 2 with the main mass of the medullary substance of the posterior lobe. It undergoes a rather simple type of division, and its upper part participates materially in the curving loop of the vermal pattern. Ray B arises as a single slender stem below the origin of ray C, undergoes simple division and presents only a few lateral branches. Ray A consists

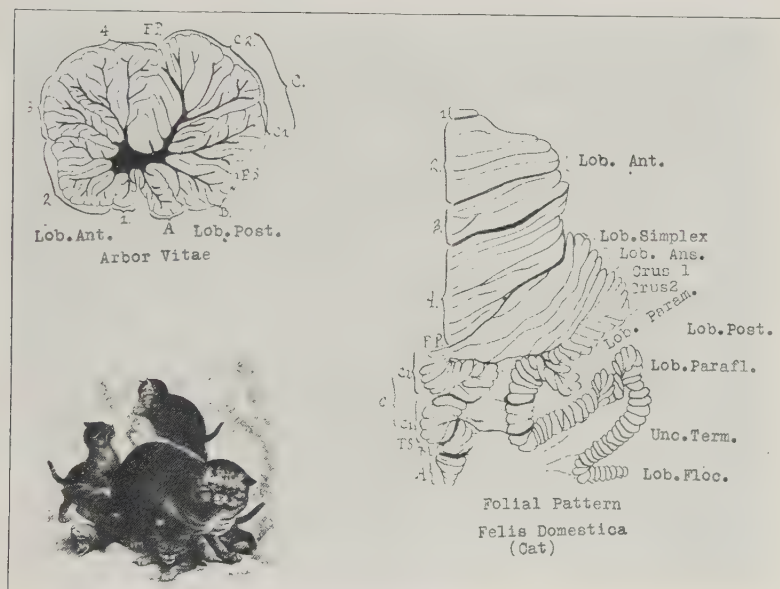


FIG. 15. *Felis domestica* (cat)

of a single stem which presents a few simple side twigs and ends in a bifurcated termination.

The lobules

The lobules produced by the division of the medullary substance into the medullary rays is made up of a simple lobulus 1, consisting of a single surface folium; a more complicated lobulus 2, which has three medullary rays as its basis, and presents an increasing series of surface folia; a lobulus 3, apparently from its origin, and independent lobulus comprised of a few simple folia, and lobulus 4, which presents three chief subdivisions. It forms the cephalic limit of the fissura primaria and is simple in its composition. Lobulus C is subdivided into lobuli C 2 and C 1.

Lobulus C 2 presents a number of cephalic folia in the depths of the fissura primaria and a group of surface folia, the most cephalic of which have the usual transverse arrangement, while the caudal group represents the beginning of a rather simple vermal twist in the region of lobuli C 1 and C 2. Between lobulus C 1 and lobulus C 2 there are a number of submerged folia which are interested in the formation of the twisting vermal turn. Lobulus C 1 is relatively simple in the arbor pattern, but presents a considerable degree of convolution in the folial pattern. Lobulus B is a simple lobulus consisting of three or four folia. Lobulus A is an uncomplicated lobulus presenting only two or three surface folia.

The folial pattern of Felis domestica

The cat presents a rather simple folial pattern. The anterior lobe is relatively extensive in the folial pattern, occupying at least half of the surface of the cerebellum. The fissura primaria, which limits the anterior lobe caudally, is relatively simple and extends outward on the hemispherical surface, gradually inclining forward to the periphery. The fissura secunda appears in rather an oblique position separating lobuli C and B. Its continuation outward seems to mark off the paramedian from the parafoccular formation. Lobulus 1 apparently is confined entirely to the vermis and consists of a single surface folium. Lobulus 2 presents a number of vermal subdivisions which become lost as the folia are followed outward into the hemisphere. The folia show a definite tendency to condensation toward the periphery. Lobulus 1 and lobulus 2 are inserted by means of a common medullary stem into the underlying white substance. Lobulus 3 is a simple lobulus consisting of three folia, which are reduced to two and inserted by an independent peduncle. Lobulus 4 consists of a group of parallel folia, there being but little reduplication in the vermis region and only a slight reduction in the number of folia constituting the lateral portion of the lobulus. Lobulus C can be divided into two divisions. A cephalic group of two folia, which are continued outward as simple folia arranged in a parallel fashion, corresponds to the lobulus simplex. The rest of the vermis forms an S-shaped turn, the first limb of the S being to the left, crossing to the right and then again to the left, the apex of the curve being in all cases on one side or the other of the midline. The lateral portion of lobulus C presents a fairly complicated arrangement with a definite lobulus ansiformis and the development of crus 1 and crus 2, and the formation of a sulcus intercruralis. Crus 1 continues with rapidly shortening folia, the apex of the ansiform arrangement being produced by a rosette, following which appears crus 2 which rapidly returns along the course of the folia of crus 1. At its transition into the lobulus paramedianus, a definite folial rosette appears. The lobulus paramedianus is connected with the caudal vermal portion of lobulus C 2 and with lobulus C 1 and presents a regular series of folia which continues backward to the position of the fissura secunda where the folial chain turns on itself and continues out into the lobulus parafoccularis. The folial chain, following the S-shaped loop forming the major portion of lobulus C, returns to the midline and presents a few simple successive folia corresponding to lobulus B. Lobulus B is based on a peduncle which is continued outward in the general direction of the lobulus parafoccularis. The lobulus parafoccularis arises as a chain of lamellae directly continuous with the lobulus paramedianus and continues

forward. As it curves around the lobulus ansiformis it develops a double group of roests. The lamellar chain then continues backward paralleling its previous course outward and ends in a long chain of folia, the uncus terminalis. The lobulus parafloccularis occupies the usual position seen in the carnivore type of cerebellum, being situated ventral and lateral to the general group forming the lobulus simplex, lobulus ansiformis and lobulus paramedianus. Lobulus A consists of a simple group of rapidly diminishing vermal folia. It is continued outward in an ill defined peduncle in the general direction of the lobulus floccularis. The lobulus floccularis appears as a simple group of folia directly following the uncus terminalis. The lateral extensions of lobulus C are inserted by a large peduncle into the medullary substance, while the parafloccular formation is inserted by an extended application of the folia to the medullary substance. The lobulus floccularis lies in the usual position between the peduncle of the cerebellum and the parafloccular formation.

Lobuli 1 and 2 have a common peduncular implantation into the medullary substance. Lobulus 3 and lobulus 4 share a broad attachment. Lobulus C has one broad medullary implantation, with the paraflocculus lateral and ventral to lobulus C.

Physical characteristics of Felis domestica

The cat family all present similar characteristics and vary chiefly in size, ranging from the full grown lion or tiger to the small cat. The head is rounded, with a short jaw, and the eyes are placed well forward so that the visual fields are overlapping. The eyes are conjugated in their movements. The ears are of medium size, rounded and fairly movable. The tongue is large but not prehensile. The neck is short and presents a considerable range of movement. The limbs are short and exceedingly powerful in the largest member of the family. The body is heavy and rather elongated. The tail is long and is apparently of some equilibratory use in the animal's flying leaps. The members of the family in general are possessed of an extreme degree of grace, agility and perfection of timing and rhythm. They are extremely agile and active to a degree. They cannot maintain a rapid pace in running for any great distance, but their movements of attack and defense are of unbelievable rapidity and precision. The four limbs are used in locomotion, but all are capable of a certain degree of unilateral independence which is, of course, much greater in the fore limbs.

CANIS LATRANS (COYOTE)

The arbor vitae of the coyote presents a more or less quadrilateral form. The fissura primaria appears somewhat behind the middle and is directed downward and forward toward the ventricular fastigium which is placed rather cephalad to the middle of the lower part of the arbor pattern and is relatively wide open. The line of the fastigium and fissura is more or less oblique from behind, forward and downward. The fissura secunda appears between lobuli B and C and is somewhat below the level of the medullary substance. The arrangement of the fissura primaria and the fastigium divides the median section of the cerebellar vermis into more or less equal halves, the fissura primaria, however, as already indicated, being rather oblique from behind, forward and downward, owing to the overgrowth

of lobulus 4. The medullary substance appears consolidated in the anterior lobe, being a large, heavy mass with a caudal termination markedly constricted by the fissura primaria and the ventricular fastigium, and it is drawn out into the posterior lobe, supplying the framework of that lobe.

The medullary rays

Ray 1 is a narrow stalk, arising close to the ventricular fastigium, and giving off simple side branches. Ray 2 consists of the extension forward of the anterior medullary substance, and gives rise to two branches, each forming a subdivision

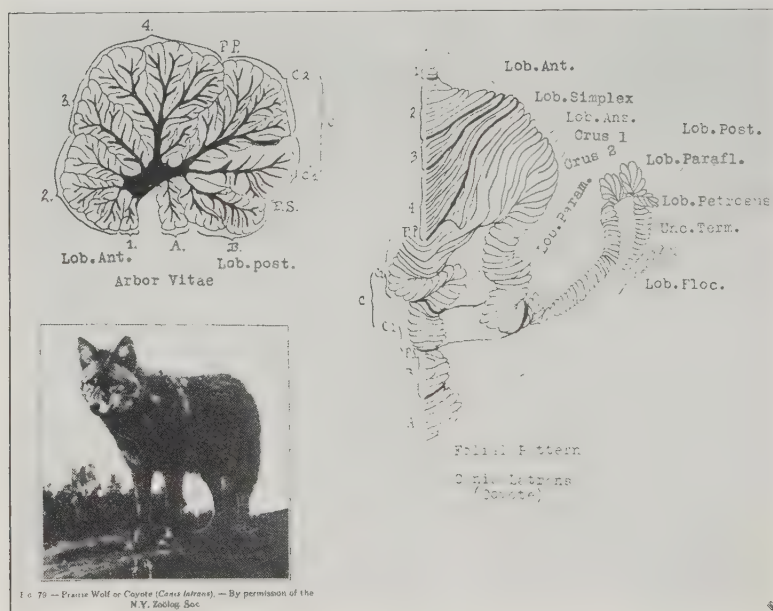


FIG. 16. *Canis latrans* (coyote)

of lobulus 2. The first of these immediately divides into two stems which diverge and give off rather numerous twigs, while the dorsal branch does not divide until near its termination and gives off relatively few side shoots. Ray 3 arises as an apparently independent ray from the substance of the medullary center between the origin of the groups of rays forming ray 2 and ray 4. It arises as a large stalk directed forward, giving off simple side branches, and ends in a terminal bifurcation. Ray 4 consists of a heavy prolongation upward of the medullary substance. It arises almost vertically above the fastigium, giving off a number of simple branches, and then divides into three subdivisions, each of which is extensively subdivided. In the depths of the fissura primaria, ray 4 gives off one major caudal stem. The

posterior medullary substance consists of a continuation backward of the anterior medullary substance as a somewhat attenuated mass, which almost immediately divides into three terminal branches forming rays C 2, C 1 and B. Ray C 2, the stoutest of the three, is the chief continuation caudally of the medullary substance of the lobe and gives off a number of subsidiary branches which are hidden in the depths of the fissura primaria. It subdivides into four chief rays which form a terminal spray producing the surface configuration of lobulus C 2. The last ray, which does not quite reach the surface, does not present any lateral derivatives and is apparently concerned in the sigmoid twist of the vermis, forming the stem for the mass of folia producing one of the curves in the vermal pattern. Ray C 1 arises just below the origin of ray C 2, gives off lateral branches and then divides into a series of branches which appear as serial lamellae in the folial pattern. Ray B arises still further caudally below the origin of rays C 1 and C 2. It almost immediately divides into two branches, a large dorsal and a smaller ventral stalk, the former giving rise to a considerably greater number of twigs. Ray A is a simple stalk arising close to the caudal boundary of the ventricular fastigium.

The lobules

Lobulus 1 is small with only two or three minor folia. Lobulus 2 is considerably larger and consists of three distinct portions which, however, do not show any particular distinguishing characteristics. Lobulus 3 is a simple lobulus with five surface folia. Lobulus 4 is extensive on the vermal surface, and presents three definite subdivisions as a result of this division of ray 4. Lobulus C is divided, as are the rays, into lobulus C 2 and lobulus C 1. Lobulus C 2 is rather more extensive and consists of three portions corresponding with the branches of the medullary ray. The varying characteristics of these are seen in the folial pattern, the first corresponding to the lobulus simplex and the second to the twisting vermal pattern. The under surface of ray C 2 gives rise to three or four folia which are continued outward to form the stem of the twist in the vermis. Lobulus C 1 is a conical shaped lobulus which caudally presents an extensive group of folia. Lobulus B presents two definite subdivisions but consists only of serial folia. Lobulus A is relatively insignificant and is formed by a simple group of folia on a single stem.

The folial pattern of Canis latrans

The pattern of the coyote is an arrangement of folia and lobules typical of carnivorous animals. The fissura primaria separating the anterior and posterior lobes arises from about the midpoint of the vermis and proceeds outward in a relatively simple form, directed considerably forward, so that the lateral extent of the lobe is much less than its extent at the midline. The fissura secunda appears in its usual position between lobuli B and C and is continued outward into the folial pattern to the junction of the lobulus paramedianus and the lobulus parafloccularis. The anterior lobe is fairly simple and consists of a series of folia presenting a gradually increasing width. The folial arrangement of the posterior lobe is characteristic of the typical pattern for carnivorous animals, presenting a fairly diagrammatic disposition of all of the various components of the lobulus complicatus.

Lobulus 1 consists of three simple vermal folia. The folia of lobulus 2 present a considerable vermal differentiation and lateral extensions which successively increase the caudalmost folium showing the greatest lateral disposition. There are a number of short vermal sulci. Lobulus 3 is simple and narrow, consisting of only one complete folium which is subdivided mesially into at least five subsidiary folia. Lobulus 4 presents a similar arrangement, the peripheral portion consisting of only two folia which are increased to ten or a dozen at the midline by the appearance of short vermal sulci.

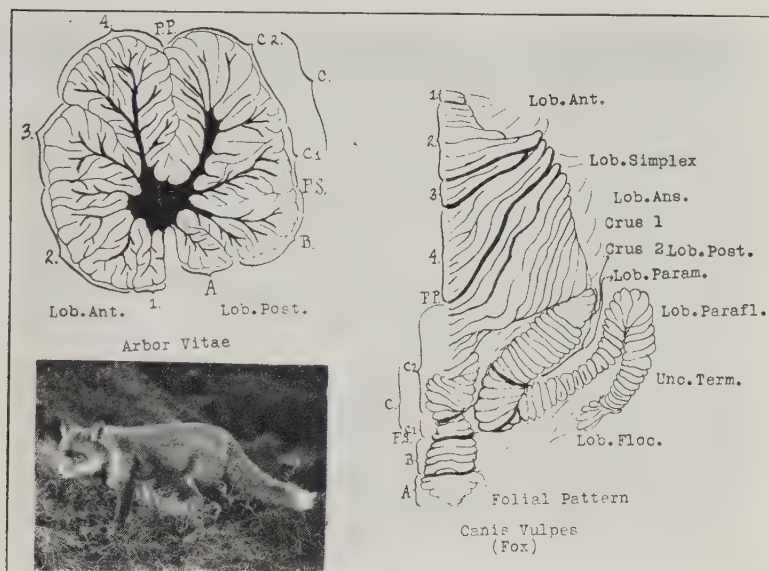
The posterior lobe is characteristic. The cephalic portion of lobulus C 2 is relatively simple in its vermal division. It consists of a number of folia which run from the midline to the periphery without any material irregularity in their disposition. As they are continued outward into the lateral hemisphere, they are displaced somewhat backward by a group of folia which emerge from the depths of the fissura primaria, corresponding to the submerged group of folia in the fissure arising from the cephalic aspect of ray C 2. These folia represent the lobulus simplex. The caudal portion of the vermis of lobulus C 2 shows a characteristic S-shaped twist which begins on the right side of the vermis, crosses to the left and returns to the right and then to the midline. The portion of the twisted vermal lamellar chain is connected laterally with the lobulus ansiformis and the lobulus paramedianus.

Succeeding the simply arranged lobulus simplex, a group of folia appears which passes outward into crus 1 of the lobulus ansiformis. These folia decrease in extent until the apex of the lobulus ansiformis is reached, where the lamellar chain turns on itself and returns toward the midline, forming crus 2, and a distinct intercrural sulcus. Arriving in the paramedian position, crus 2 turns backward, straightening out into a well defined lobulus paramedianus, and continues caudally with only a slight interruption in the middle, representing an abortive attempt at a roset formation, to become continuous with the lobulus parafoccularis. Lobulus C is a simple, straight collection of vermal folia, the caudal continuation of the S-shaped curve of lobulus C 2. This simple folial chain is connected across the paramedian fissure with the terminal folia of the lobulus paramedianus as it merges with the lobulus parafoccularis. Lobulus B presents a simple series of five or six vermal folia. It is apparently connected by a peduncle with the parafoccular formation. The parafocculus begins at the termination of the lobulus paramedianus, and is separated from it by the fissura secunda. It immediately develops a folia roset; then there follows a long, straight chain of folia which continues around crus 2 and crus 1 almost to the anterior lobe. It here turns on itself forming a double series of rosettes and then a distinct protrusion outward as a rosette forming a distinct lobulus petrosus. This is completed by the uncus terminalis. Lobulus A presents a vermal rosette the peduncle of which is continued outward toward the lobulus floccularis which consists of a short folial chain and rosette situated in its usual position between the cerebellar peduncle and the lobulus parafoccularis.

The various lobuli of the anterior and posterior lobes show a relatively simple arrangement of their implantation into the medullary substance. Lobuli 1 and 2 are implanted together; lobulus 3 and lobulus 4 are implanted together, and the lobuli simplex, ansiformis and paramedianus have a broad support on the medullary substance, lateral and ventral to which is inserted the entire length of the lobulus parafoccularis and the uncus terminalis.

Physical characteristics of Canis latrans

The coyote has the typical body form of the domestic dog, well developed and carried on four relatively short legs. The neck is short but quite mobile. The eyes occupy an anterior position, possess overlapping fields of vision and are well conjugated in their movements. The tail is bushy and has no particular characteristics beyond that of utility. The animal is swift, possessing a considerable degree of speed without, however, the extreme agility and acrobatic powers of the cat family. There is some unilateral independence in the movements of the legs, but they are used chiefly for locomotion and for digging in the ground. The coyote's need for equilibrium is moderate.

FIG. 17. *Canis vulpes* (fox)

CANIS VULPES (FOX)

The arbor vitae of the fox is roughly quadrilateral in form, being somewhat greater in its vertical than its horizontal diameter. The fissura primaria is almost vertical and is situated directly above the fastigium which is vertical and fairly wide. The fissura secunda appears in its usual position and is almost in direct continuation backward of the axis of the medullary substance. The arbor vitae is divided into approximately equal anterior and posterior lobes by the approach of the fissura primaria to the ventricular fastigium. The medullary substance is collected chiefly in the center of the anterior lobe as a large mass of white matter, being continued backward as an attenuating structure which is continued upward into ray C 2.

The medullary rays

The medullary rays are relatively slight except ray 4 and ray C 2, and the arbor vitae is similar to that structure as it appears in *Felidae*. Ray 1 arises as a slender branch from the ventral surface of the medullary substance and gives off two simple series of side branches. The medullary rays forming lobulus 2 arise as three independent branches from a rather thick extension forward of the medullary substance, and divide the lobule into three parts. They are all slender and give off relatively few secondary branches, the first two undergoing secondary division. Ray 3 does not have an entirely independent origin, but arises from the base of ray 4. It is a slender, arched ray, giving off a number of side branches. The independence of this ray can be questioned, and it may be more correct to call it ray 4 A as it indubitably belongs to the ray 4 complex. Ray 4 is considerably heavier, is almost vertical and arises from about the center of the medullary substance of the anterior lobe by means of a rather heavy extension upward of the medullary substance. It gives off cephalic and caudal branches and subdivides into two chief stalks which give off lateral shoots as they proceed to their terminal branches. Ray C arises as a single prolongation backward of the medullary substance which almost immediately divides into two branches, rays C 2 and C 1. Ray C 2 is continued upward and backward in an arched fashion, giving off cephalic and caudal branches and then breaking up into a number of simple terminal twigs, some of which undergo further slight division. One of the caudal branches presents a rather extensive division. Ray C 1 is a relatively slender ray, giving off side branches and terminating in three small twigs. Ray B arises from the caudal portion of the medullary substance of the posterior lobe, and subdivides into two chief branches, the dorsal division being much the longer and giving rise to a fair number of twigs. Ray A is a simple stalk arising close to the caudal boundary of the fastigium, presenting a few lateral branches.

The lobules

The lobules produced by the division of the medullary substance are rather extensive and present a considerable degree of complexity. Lobulus 1 is relatively simple and presents a partial vermal subdivision. Lobulus 2 is considerably more highly organized and is composed of three separate sublobules, each one of which is still further subdivided, the first two being more richly foliated than the third, or most dorsal, which is quite narrow. Lobulus 3 could, with perfect propriety, be considered as only a sublobulus of lobulus 4 and termed lobulus 4 A. It is a triangular lobulus with its base at the periphery, where it is composed of a few surface folia. Lobulus 4 is relatively simple in its organization, and is composed of a number of surface folia which are divided into two groups by the terminal division of the ray and do not present definite individualities. Lobulus C. 2 presents a large number of submerged folia in the fissura primaria and a moderate number of surface folia, the cephalic of which are serially arranged, while the caudal portion begins to show the complications of the twist in the vermis in this region through the peculiar arrangement of the richly divided caudal ray and the rather large submerged ray. Lobulus C 1 consists of a small number of surface folia which

are serially arranged. Lobulus B consists of two groups of folia, owing to the division of ray B, the dorsal group being extensive. Lobulus A consists of a group of serially arranged surface folia.

The folial pattern of Canis vulpes

The folial pattern of the fox shows the usual division into the anterior and posterior lobes by means of the fissura primaria which arises at about the middle of the pattern and proceeds forward and outward in a slightly sinuous course. The fissura secunda separates lobulus C from lobulus B, and is direct'y continuous with a division in the lateral lamellar chain which corresponds to the transition from the lobulus paramedianus into the lobulus parafoccularis. Lobulus 1 is a simple, single folium which is divided in its lateral portion. This folium, however, seems to be confined to the vermis and does not present any definite contribution to the hemisphere. Lobulus 2 consists of (1) four short vermal folia, (2) two surface folia of considerably greater length which contribute to the hemisphere and (3) the most extended portion of the group, which is subdivided mesially but reduced to one folium at the periphery. Lobulus 3 consists of three folia, none of which reaches the periphery of the hemisphere, being shut off from it by the approximation of lobuli 2 and 4. It shows definite vermal and lateral portions. Lobulus 4 is extensive in the vermis, showing a number of sulci which continue for only a short distance. The folia continually decrease in number, only two folia finally reaching the periphery. The lateral extent of the anterior lobe, therefore, is much less than its median representation. Lobulus C presents a subdivision, as is shown in the arbor vitae, into two portions, a cephalic portion, which corresponds to ray C 2, and a caudal portion, which corresponds to ray C 1. Lobulus C 2 is again subdivided into a simple cephalic portion and a convoluted caudal portion. The cephalic folia proceed outward in a simple fashion into the hemisphere, forming a definite lobulus simplex. Succeeding the lobulus simplex is a group of progressively diminishing folia which form crus 1 of the lobulus ansiformis. Reaching the apex of the ansiform formation, the lamellar chain turns caudally and mesially forming a well defined crus 2, which, by its approximation to crus 1, forms an intercrural sulcus. The folial chain of crus 2 then turns backward into a simple paramedian formation in close proximity to the caudal and vermal portion of lobulus C 2 and lobulus C 1, with which it is connected. Lobulus C 1 consists of three small folia which are continuous with the most caudal folia of the paramedian formation. Lobulus B consists of four or five fairly wide folia which converge on a peduncle that continues outward and approaches the base of the paramedian formation. The lobulus parafoccularis arises as a direct continuation of the folial chain of the paramedian formation. It appears as a simple chain of lamellae, which turns on itself in the region of the apex of the lobulus ansiformis, and is continued backward into an uncus terminalis. Lobulus A consists of five or six serial vermal folia set on a single peduncle which is continued outward in the general direction of the lobulus floccularis, which succeeds the uncus terminalis and is situated between the peduncle of the cerebellum and the parafoccular formation, being made up of a single folial rosette.

The implantation of the various lobules in the medullary substance is relatively

simple. Lobuli 1, 2 and 3 have a single peduncle. Lobulus 4 is more or less separate, while lobulus simplex, lobulus ansiformis and lobulus paramedianus are directly implanted by a broad base on the medullary substance, lateral and ventral to which is the broad attachment of the lobulus parafoccularis and the uncus terminalis.

Physical characteristics of Canis vulpes

The fox is small and not so heavily built as most of the dog family. It presents a somewhat elongated body, set on four slender legs; it has a moderately developed, mobile neck, a small head, eyes set well forward and quite movable triangular ears. The legs are about medium length, while the tail is long and bushy. The fox possesses a considerable degree of speed and agility. The eye movements are well conjugated and the visual fields are overlapping. The fox is capable of climbing trees with ease and celerity. The prey of the fox consists largely of mice and birds, so that it is evident that he is able to move with extreme speed and accuracy, and that the fore limbs are capable of a considerable degree of unilateral independence in their ability to catch and hold these small and relatively quick-moving victims.

CERCOLEPTES CAUDIVOLVULUS (KINKAJOU)

The arbor vitae of the kinkajou presents an oval form. It is subdivided into about equal anterior and posterior lobes by an almost vertical fissura primaria and a wide open ventricular fastigium. The fissura secunda appears in the usual position as a direct backward continuation of the axis of the medullary substance, its disposition being backward and somewhat upward. The fissura primaria and the ventricular fastigium divide the arbor vitae into approximately equal posterior and anterior lobes. The appearance of the arbor vitae is relatively light and delicate, the foliation not being extensive. The medullary substance presents a marked condensation in the anterior lobe, a distinct constriction at the isthmus between the anterior and posterior lobes and a short caudal prolongation which is chiefly concerned in the origin of ray C.

The medullary rays

The division of the medullary substance into medullary rays is fairly simple, there being no great degree of secondary subdivision. Ray 1 appears as an unbranched stem from the ventral surface of the medullary substance. The entire medullary substance is drawn forward into the base of lobulus 2. Three rays appear to form lobulus 2, the first two being relatively simple and presenting only a few branches. The third stem might easily form an independent ray 3 if its origin occurred only a little more caudally. This ray is somewhat heavier, divides into two branches and is provided with a number of lateral twigs. Ray 4 arises vertically, as a somewhat heavier stalk, from the medullary substance, and divides into two branches, one of which proceeds cephalically and the other upward. Both of these subdivide and give off lateral branches. Ray C 2 and ray C 1 arise together as a prolongation upward and backward from the medullary substance of

the posterior lobe, with a heavy base giving origin to the two branches which diverge from one another. Ray C 2 gives off one stalk in the depths of the fissura primaria, and another, which, reaching the periphery of the arbor vitae, subdivides into a spray of terminal branches characteristic of the twisted form of the vermis. A number of small branches arise from its caudal surface. Ray C 1 arises as a straight stalk with lateral branches and divides into a terminal division of three stems. Ray B arises as a direct continuation caudally of the medullary substance of the posterior lobe. It gives off lateral branches and then divides terminally. Ray A arises from the under surface of the medullary substance close to the ventricular fastigium and gives off a series of lateral branches.

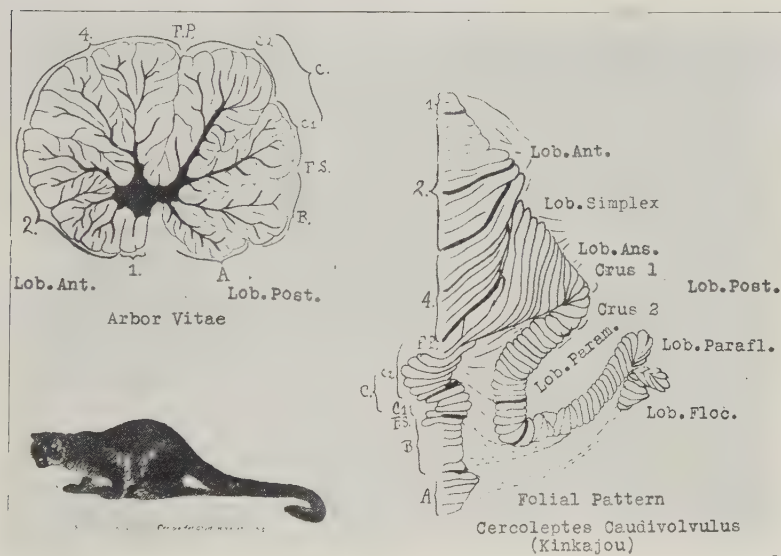


FIG. 18. *Cercoleptes caudivolvulus* (kinkajou)

The lobules

Lobulus 1 consists of a single folium forming the cephalic margin of the fastigium. Lobulus 2 presents three subdivisions; the first two are simple, while the third is larger and heavier and consists of two definite divisions. This portion of lobulus 2 corresponds to the structure called lobulus 3 in other arbor patterns when the base of the ray arises slightly more caudally. Lobulus 4 consists of two portions which do not present any particular peculiarities, except that each one is further divided into two folial groups. Lobulus C is divided into two parts. Lobulus C 2 is well defined and presents a few regular cephalic folia in the fissura primarius and a number of irregular caudal folia which participate in the vermal twist as is evident from the appearance of the surface folia that form the summit

of the lobulus. Lobulus C 1 is simple and is made up of a few regular submerged and surface folia. Lobulus B consists of a series of surface folia divided into two groups. Lobulus A is a fairly well developed elongated lobulus forming the caudal boundary of the fastigium.

The folial pattern in Cercoleptes caudivolvulus

The pattern is comparatively uncomplicated. The fissura primaria appears somewhat caudal to the middle of the vermal disposition of the folia. It proceeds laterally and then turns rather abruptly forward. The fissura secunda appears in its usual position between lobuli B and C and is continuous with a sulcus which separates the paramedian formation from the lobulus parafloccularis. Lobulus 1 consists of a single vermal folium with a short medial sulcus. Lobulus 2 consists of a series of folia divided into two folial groups, increasing in their lateral extent, showing in the caudal folia definite vermal and lateral portions. The caudal division is compressed by lobulus 4, only one of the folia reaching the periphery. Lobulus 4 consists of a series of simple folia, only one of which appears definitely at the periphery, the rest disappearing in the fissura primaria. Lobulus C consists of two definite portions. The cephalic subdivision shows a further differentiation into (1) a portion the folia of which appear in the vermal region and continue outward into the lateral part of the lobule, a number of them converging on the fissura primaria; and (2) a caudal portion in which the vermal and lateral portions of the folia are not directly continuous but are divided by a definite paramedian sulcus. One of the folia of the cephalic portion can be traced from the vermis to the periphery—apparently the lobulus simplex. The rest of the vermis of lobulus C, comprising the caudal portion of lobulus C 2 and lobulus C 1, presents a simple curve originating on the left hand side of the vermis and extending over to the right of the midline for a short distance. These folia are continuous with the folia of the lobulus ansiformis and the first portion of the lobulus paramedianus. The folia which directly succeed the single folium of the lobulus simplex form a diminishing group comprising crus 1. This terminates at the apex of the lobulus ansiformis as a rosette, crus 2 then continuing mesially in contact with crus 1 and forming a fairly definite intercrural sulcus. The transition from crus 2 to the lobulus paramedianus is gradual as the folial chain approaches the vermis. It then turns backward and forms a series of folia connected with the vermal portion of C 1, the lobulus paramedianus. Lobulus B consists of a group of vermal folia. They surmount a definite peduncle which is continued outward toward the origin of the lobulus parafloccularis. The lobulus parafloccularis is separated from the lobulus paramedianus by the fissura secunda, presents an abortive rosette and then continues forward and outward as a simple folial chain which reaches the apex of the lobulus ansiformis and then turns back on itself, ending in a short uncus terminalis. Lobulus A consists of a simple series of vermal folia resting on a peduncle which extends outward in the direction of the lobulus floccularis. The lobulus floccularis appears as a definite rosette and a small number of rapidly diminishing folia.

The folia of lobuli 1 and 2 and the cephalic folia of lobulus 4 are inserted into the medullary substance by means of a common peduncle. The lobulus ansiformis and lobulus paramedianus are supplied with a broad implantation into the medul-

lary substance, the parafloccular formation being connected with the medullary substance lateral and ventral to the medullary insertion of the anterior lobe and the cephalic portion of the posterior lobe.

Physical characteristics of Cercoleptes caudivolvulus

The kinkajou is a small carnivorous animal with a catlike form, a small body and a relatively long neck. The eyes are situated well forward with overlapping fields of vision, and are well conjugated in their movements. The ears are quite feline and freely movable. The limbs are catlike in appearance and function, but the animal is much stronger than cats of its own size. The kinkajou is actively arboreal in its habitat, is a fearless climber and possesses a tail which is about equal to the length of its body and is actively prehensile. The fore limbs, which can be used as hands with facility, present great unilateral independence, equal to that of the lemurs with which this animal was originally placed. It possesses a long tongue which is protrudable and with which it licks up insects. The kinkajou is able to catch birds and small mammals. It is capable of great rapidity and agility of movement. Its activities are chiefly nocturnal.

NASUA RUFA (COATI)

The arbor vitae of the coati presents a relatively simple arrangement and is somewhat pyramidal in form. The fissura primaria is situated about in the middle; it is quite vertical and approaches almost directly the ventricular fastigium, which is pyramidal in form. The division by the fissura primaria and the ventricular fastigium into anterior and posterior lobes is about equal. The fissura secunda appears in the usual position low down in the posterior lobe and is in direct continuation with the axis of the medullary substance. The medullary substance presents its major portion in the anterior lobe as a rather thick, heavy mass which is continued upward as a strong process into lobulus 4. The posterior portion of the medullary substance continues upward as a well defined prolongation into lobulus C 2 which, together with ray 4, presents a U-shaped distribution of the medullary substance. The remainder of the medullary rays are slender.

The medullary rays

Ray 1 consists of a single unbranched process from the ventral surface of the anterior medullary substance. Ray 2 consists of a prolongation of the medullary substance cephalically, which gives rise to three independent branches, the first of which is quite simple, the second more extensive and subdivided and the third or dorsal branch intermediate in complexity between the first two stems. The next branch is one which resembles ray 3, but as it arises from the base of ray 4 it is considered as an integral part of ray 4. It arises close to the base of ray 4 at its junction with the mass of the medullary substance. It is arched forward as a slender fasciculus presenting only a few side-branches. Ray 4 itself is a massive prolongation upward of the medullary substance, which subdivides into four slender branches. The first two arise together and undergo a meager further division; the third is an apical branch which is divided and gives origin to only a few branches,

and the fourth is a simple ray in the depths of the fissura primaria. Ray C 2 is heavy, and is a continuation upward and backward of the medullary substance of the posterior lobe. It presents a small number of cephalic branches and divides at its summit into a spray of four branches which undergo further subdivision. The caudal surface of ray C 2 gives rise to a number of smaller branches in the depths of the fissure separating lobulus C 2 from lobulus C 1. Ray C 1 is a slender branch, a direct continuation caudally of the medullary substance which presents only a few lateral branches and ends in a simple bifurcation. Ray B is a bare caudal branch of the medullary substance which subdivides into two simple divisions. Ray A is a slender fasciculus close to the ventricular fastigium which presents only cephalic branches and a terminal bifurcation.

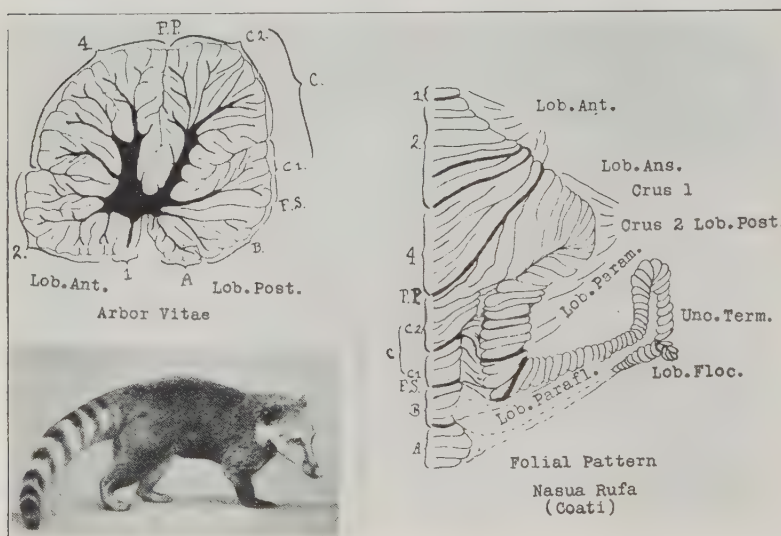


FIG. 19. *Nasua rufa* (coati)

The lobules

Lobulus 1 is composed of a simple undivided folium which forms the cephalic wall of the ventricular fastigium. Lobulus 2 is more complicated and consists of three folial groups. The first presents a single subdivided folium, the second is composed of two folial collections and the third is much more distinct and made up of two folia. Lobulus 4 presents a distinctly curved cephalic surface and a straight caudal surface formed by the fissura primaria. It is subdivided into three chief folial groups which increase in size from before backward. The lobulus presents a considerable number of folia submerged in the fissura primaria. Lobulus C presents a rather similar reverse picture to lobulus 4, its cephalic surface being straight, and its caudal outline curved. Lobulus C 2 is much larger than lobulus

C 1 and is conical in shape, the folial arrangement being rather simple and uncomplicated. Lobulus C 1 is conical in form and appears meager in its composition. Lobulus B is simple and is made up of two folial groups. Lobulus A is somewhat elongated caudally and does not possess any particular individualities.

The folial pattern of Nasua rufa

The folial pattern presents a relatively simple type of organization. The fissura primaria starts at about the midpoint of the pattern and proceeds forward and outward. The anterior lobe is distinctly triangular in outline while the posterior lobe is simple, the vermal folial chain being straight, without any lateral deviation or curve. The fissura secunda appears in the usual position between lobuli C and B, and is continuous with the sulcus which separates the lobulus paramedianus from the parafloccular formation. Lobulus 1 consists of a single vermal folium. The folia of lobulus 2 are successively extended and arranged in a gradually increasing series with a caudal folial group which is rather distinct from the remainder of the lobulus. There is no vermal division of this lobule by secondary sulci. Lobulus 4 consists of a group of folia, eight or nine in number, at the median line which are reduced to two at the periphery. Some of the sulci are purely vermal; others extend further outward. The reduction in the number of folia forming the lateral portion of the anterior lobe accounts for the convergent direction of the sulci. Lobulus C 2 is divided into two definite portions, the cephalic group of folia being directly continuous with the vermal folia and converging on the fissura primaria, disappearing in it without reaching the periphery. There is not, therefore, a definite lobulus simplex. Following these folia which disappear in the fissura primaria, there is a series of folia, gradually diminishing in length, which form crus 1 of the lobulus ansiformis. The apex is formed by a folial rosette, following which appear the folia of crus 2 which turn backward, mesially and caudally, their mesial extremities being in contact with crus 1 and thus forming a well defined sulcus intercruralis. The caudal half of the vermal portion of lobulus C 2 consists of a group of folia which are confined to the vermis, but which are continuous in the depths of the paramedian fissure, with the proximal folia of crus 2. Lobulus C 1 consists of three or four vermal folia which succeed the folia of lobulus C 2 in a direct line. These are connected with the folia of the lobulus paramedianus, as far back as the fissura secunda. The folia of lobulus B are arranged in a simple chain, and converge on a peduncle which is directed outward toward the lobulus parafloccularis. The lobulus parafloccularis is a relatively simple structure consisting of successive folia, one following the other as a definite chain. The chain turns on itself in the vicinity of the apex of the ansiform lobe, continues forward, turns again on itself and then continues backward and mesially in the form of an uncus terminalis. Lobulus A consists of four or five simple folia arranged on a peduncle which fades out in the medullary substance in the direction of the lobulus floccularis. The lobulus floccularis appears as a folial rosette, with a group of successively diminishing folia situated between the peduncle of the cerebellum and the parafloccular formation.

The implantation of the various lobules is relatively simple, the first, second, third and fourth all converging on a single peduncle. The lobulus ansiformis

and the lobulus paramedianus are inserted by a converging peduncle, lateral and ventral to which are attached along the surface of the medullary substance, the parafloccular formation and the uncus terminalis.

Physical characteristics of Nasua rufa

The red coati is a small bodied carnivore combining the physical characteristics of a cat and a badger. It is actively arboreal and chiefly nocturnal. The body is rather socky, the limbs short and powerful, the neck of medium length and the head of moderate size. The eyes are placed anteriorly, possess overlapping fields of vision and are well conjugated in their movements. The head is continued forward into a well defined proboscis which is actively movable and is used in grubbing up insects, larvae, etc. The tongue is of moderate size and is used in lapping up water. The coati descends a tree head first, regulating its descent by its hind limbs which are flexible and agile. It has a relatively long tail which does not seem to be of any particular use or function and is not prehensile.

URSUS AMERICANUS (BLACK BEAR)

The arbor vitae of the black bear presents a more or less rounded outline. The fissura primaria appears somewhat caudal to the middle of the arbor and approaches the medullary substance somewhat behind the point at which the narrow ventricular fastigium appears. It is directed somewhat from behind forward and downward, its lower extremity turning rather sharply forward. This arrangement of the fissura primaria and the fastigium divide the arbor in rather an oblique manner into the anterior and posterior lobes, the former being somewhat the larger. The fissura secunda appears below the middle of the posterior lobe, directed in the axis of the medullary substance backward and somewhat downward toward the periphery. The medullary substance appears as a rather large mass in the center of the cerebellum, not showing any particular demarcation into the medullary substance of the anterior and posterior lobes. The arbor pattern in general shows a rather extensive degree of lobulation, the medullary rays being fairly heavy with numerous subdivisions.

The medullary rays

Ray 1 appears just in front of the fastigium as a simple stalk, with a few lateral branches. Ray 2 is comprised of three independent stems which arise from a heavy prolongation forward of the medullary substance. The first is directed almost immediately downward and divides into a terminal bifurcation without any side branches. The second, which is heavy, is directed forward and presents a division at its tip into three medullary twigs, which do not give off lateral branches but have terminal bifurcations. The third subdivision of ray 2 appears in a more or less semi-independent position between the base of ray 2 and the base of ray 4. It is a relatively heavy stalk, advancing upward and forward, and it gives off a prominent cephalic branch which divides into lateral twigs, and a more vertical stem which presents lateral and terminal branches. Ray 4 is a heavy stalk arising from the upper aspect of the medullary substance. It is almost vertical dividing into two

heavy stems which diverge. The cephalic stem proceeds somewhat forward and upward, giving off a few simple divisions and ending in three terminal branches. The caudal stem of ray 4 is a rather heavy stalk almost devoid of cephalic branches except at its summit, while from its caudal aspect arise a considerable number of long branches which proceed backward toward the fissura primaria. A number of slender branches arise from the medullary substance in the depths of the fissura primaria. Ray C appears as the main prolongation of the posterior portion of the medullary substance, immediately subdividing into two major stalks, rays C 1 and

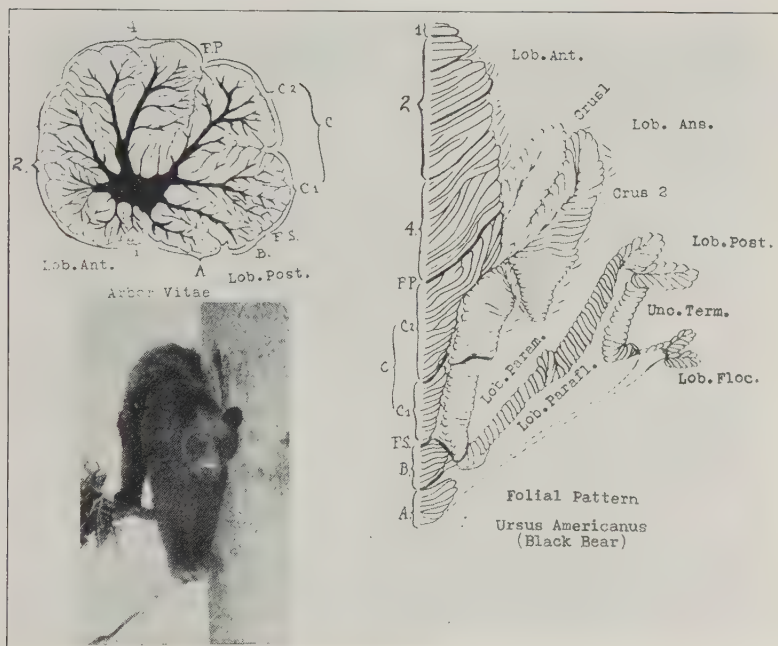


FIG. 20. *Ursus americanus* (black bear)

C 2. Ray C 2 proceeds upward and backward, giving off minor stems as it proceeds, and then divides into a cluster of branches at its summit. Ray C 1 proceeds almost directly backward, giving off a few slender lateral branches, and then divides into a group of rather extensively divided subrays. Ray B arises below the fissura secunda as a slender, simple ray, giving off lateral branches. Ray A is a simple derivative of the medullary substance, with a few side branches.

The lobules

The lobules are disposed in accordance with the branches of the medullary substance already described. Lobulus 1 is simple, presenting only a small degree

of division. Lobulus 2 comprises the major subdivision of the anterior lobe. Its base is formed by the forward extension of the entire medullary substance of the anterior lobe. It is subdivided into three subordinate portions by the disposition of the medullary rays. The first is formed of two groups of folia, while the second is more extensive and comprises three folial clusters. The third subdivision possesses the characteristics of lobulus 3 and would be recognized as a separate lobulus, were the origin of its ray not in such close relationship to the other rays forming lobulus 2. It is composed of two groups of surface folia. Lobulus 4 is relatively conspicuous, consisting of two sublobules: the cephalic group made up of a fairly extensive series of surface folia, while the caudal collection presents a small cephalic group of folia and a series of extensive caudal branches which form the cephalic tip of the fissura primaria. Lobulus C consists of two portions, lobuli C 2 and C 1. Lobulus C 2 is a relatively extensive lobulus forming the dorsocaudal angle of the arbor vitae, and presents a number of vermal subdivisions. Lobulus C 1 is somewhat more extensive than usual and is formed by the three-fold division of the medullary stem into an extensive apical cluster of folia. Lobulus B is formed by a compressed group of folia, consisting of only a few surface lamellae. Lobulus A is a small lobulus and is placed almost entirely in a horizontal plane.

The folial pattern of Ursus americanus

The folial pattern of the black bear presents a general appearance which is quite individual owing to the peculiar formation of the lateral extension in the vicinity of the lobulus ansiformis. The division of the folial surface into the anterior and posterior lobes due to the fissura primaria appears in the usual position. The fissure presents itself as a relatively straight furrow beginning at about the middle of the folial pattern and proceeds outward with a considerable inclination forward. The fissura secunda appears in the usual position between lobuli B and C, and in its continuation outward divides the lobulus paramedianus from the lobulus parafoccularis.

Lobulus 1 is comparatively simple, consisting of only two vermal folia. Lobulus 2 is subdivided, as is indicated in the arboreal pattern, into three portions, a narrow group of vermal folia cephalically, a relatively wider group in the second subdivision of the lobulus and a caudal group consisting of four or five folia which proceed outward converging as they approach the periphery. Lobulus 4 presents a definite subdivision into two parts: (1) a cephalic group of striplike folia extending from the median line to the lateral periphery, the caudal folium being divided at its extremity, and (2) four or five folia which converge on the fissure separating the two portions of lobulus 4. These are succeeded by a group of folia which reach the periphery. Lobulus C presents a definite subdivision into two portions, lobuli C 2 and C 1. Lobulus C 2 consists of a group of folia, the majority of which do not reach the lateral surface, but end by turning forward into the fissura primaria. This may represent the group which usually forms the lobulus simplex. The remainder appear as short, vermal folia which come to a termination in the paramedian fissure, but are continued forward in the depths of this fissure to reappear as an elongated folial rosette. This is immediately followed by an even more

extensively developed rosette formation which appears to present some resemblance to the lobulus ansiformis, crus 1 extending outward to an apex and then returning as crus 2 which continues backward in a gradually widening series of folia. Reaching a maximum, the folia then narrow rapidly; the chain, however, at the middle of its course turns on itself in a group of submerged folia forming a rosette, and then again resumes its course backward as a typical paramedian formation. These folia are apparently continuous with the caudal vermal folia of lobulus C 2. Lobulus C 1 appears as a group of diminishing vermal folia, continuous laterally with the caudal portion of the paramedian formation, which, apparently, is a group of narrow folia terminating by junction with the lobulus parafoccularis. Lobulus B appears as a group of vermal folia arranged as a rosette, the peduncle of which is continued outward to the junction of the lobulus paramedianus with the lobulus parafoccularis. The lobulus parafoccularis runs directly forward and outward as a long chain of narrow folia interrupted at about its middle by a folial roset. It terminates as a double rosette succeeded by an uncus terminalis which, at its termination, turns outward toward the lobulus floccularis. The lobulus parafoccularis is in relationship with the lateral edge of the ansiform formation, the rosette in the lobulus parafoccularis fitting into the indentation between the caudal portion of crus 2 and the lobulus paramedianus proper. Lobulus A appears as a group of diminishing folia. These are based on a peduncle which is directed outward in the general direction of the lobulus floccularis. The lobulus floccularis consists of a simple chain of lamellae which develop two terminal rosettes.

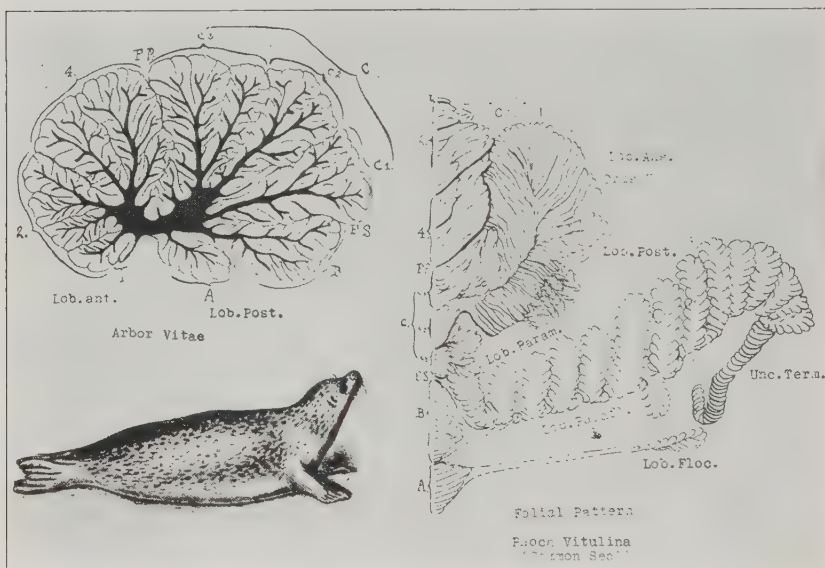
Lobulus 1 joins with the first division of lobulus 2 in its peduncular insertion into the medullary substance. The second division of lobulus 2 has an independent peduncle, while the third division has a peduncle in common with lobulus 4. The two extended rosettes and the entire paramedian formation have a common insertion, while the parafoccular formation is connected with the medullary substance, ventral and lateral to the ansiform and paramedian lobules.

Physical characteristics of Ursus americanus

The American bear is a relatively large animal about 5 feet in length and weighing about 400 pounds (181.4 Kg.). It has a heavy body, a rather large head, a thick powerful neck and short but strong limbs. The eyes are situated in the anterior position and possess overlapping fields of vision. In movement, the eyes are well conjugated. The ears are fairly large, rounded and freely movable. The limbs are powerful, and the animal is usually quadrupedal in progression, with a deliberate, flat-footed shambling gait. The bear can readily sit upright on its haunches, and it can walk upright. Under training, it can run, dance, skate and ride bicycles with the hind feet. The bear is capable of considerable speed and may even be called fleet of foot. It is a good tree climber. There is a considerable degree of unilateral independence of both the fore and the hind limbs. This is especially true of the fore limbs in digging, climbing, caring for the young and attack and defense.

PHOCA VITULINA (COMMON SEAL)

The arbor vitae of the seal shows a distinct organization of the type of carnivorous animals, with a definite division between the anterior and posterior lobes, a well defined separation of the medullary substance of the anterior and posterior lobes and a clearly marked fissura primaria and fissura secunda. The outline of the arbor vitae is relatively oval, the long diameter being directed from before backward. The fissura primaria appears well forward in the arbor vitae, and is placed more or less vertically opposite the ventricular fastigium, which is wide open, is relatively shallow and leaves a considerable extent of the medullary substance uncovered. The division into the two lobes shows a marked preponderance

FIG. 21. *Phoca vitulina* (common seal)

of material in favor of the posterior lobe. The medullary substance is definitely divided into two portions, those of the anterior and posterior lobes, by a constriction corresponding to the approach of the fissura primaria to the fastigium. The medullary substance of the posterior lobe is somewhat more extensive than that of the anterior lobe and appears chiefly as a base for the medullary rays C 2 and C 3.

The medullary rays

A distinct folium is applied to the superior medullary velum which, therefore, may be termed the lingula. If this is considered the first medullary ray, the subsequent branches of the anterior medullary substance fall into subdivisions of

ray 2. These appear as a double group of rays, the first of which arises as a stem derived directly from the cephaloventral angle of the medullary substance. The second group represents the chief prolongation of the medullary substance cephalically and presents a stout base which almost at once divides into two secondary stalks, each of which is fairly heavy. These diverge somewhat, giving off lateral branches. The first of these is considerably shorter than the second which forms the apex of the anterior lobe. The second subdivision is stout and divides into two primary subdivisions which give off lateral branches. Ray 4 appears as a vertical stalk with a heavy base which at once gives rise to three separate stalks, a cephalic which proceeds forward and upward, dividing at its extremity, a middle branch which proceeds in a curve upward and somewhat forward giving off slender branches and a caudal branch which lies in the depths of the fissura primaria. Ray C consists of almost all the medullary substance of the posterior lobe, presenting a thick, heavy center from which three chief branches arise, the most cephalic of which is a vertical continuation of the medullary center dividing into two heavy stalks which are extensively branched and bifurcate terminally. The middle branch proceeds directly backward and upward from the medullary center, giving off relatively heavy side branches and terminating in rather an extensive apical spray. The third stalk arises almost horizontally from the base of ray C, gives off lateral branches of considerable size and terminates by dividing into three subrays. Ray B is a large stalk which arises below the center of the posterior lobe, is directed almost backward, and divides into two branches. Ray A is a slender stalk arising from the ventral surface of the medullary substance of the posterior lobe and turns backward under cover of ray B.

The lobules

The lobulation of the arbor vitae depends on the subdivision of the medullary substance. Lobulus 1 consists of a single folium lying directly on the superior medullary velum, thus forming a lingula. Lobulus 2 consists of three folial groups which arise from the medullary center, the first two being narrow folial groups while the third is somewhat more extensive, presenting two distinct folial collections. Lobulus 4 is well developed and is formed by two folial groups which show a relatively rich degree of subdivision, with a considerable development of branches in the depths of the fissura primaria. Ray C forms the chief division of the posterior lobe and consists of three groups of folia which show a characteristic appearance in the folial pattern. In the arbor vitae the most cephalic is the most extensive, presenting two definite and considerable subdivisions; the second and third subdivisions are not so extensive as the first. Lobulus B is fairly well defined, divided into two chief groups of folia. Lobulus A is a well developed folial cluster forming the caudal margin of the fastigium.

The folial pattern of Phoca vitulina

The seal presents a considerable divergence from the general type of folial arrangement in carnivorous animals, in the organization of the folial pattern. In the first place, the folia are fine; the sulci separating them are wavy and broken, and many of them appear to wander about the folial surface without any definite

direction, a number turning backward almost at right angles to the general direction of the folia. There is a distinct tendency in the anterior lobe to form a vermis with definite lateral portions which faintly resembles the cetacean type of anterior lobe. The fissura primaria appears somewhat cephalad to the midpoint of the folial pattern, so that the posterior lobe is considerably more extensive than the anterior lobe. This is due to the relatively large development of the lobulus ansiformis and to the remarkable and characteristic arrangement of the paraflocculus. The fissura secunda separates lobuli B and C and the lobulus paramedianus from the lobulus parafloccularis. Lobulus 1 appears as a single folium lying on the superior medullary velum as the lingula. Lobulus 2 presents a definite subdivision into two portions. The cephalic part consists of three vermal folia subdivided at the midline. The caudal portion presents a definite development of the lateral portion of the anterior lobe but also shows clear indication of a vermian differentiation, the folia increasing in their lateral extent. Lobulus 4 is a peculiar lobulus formed of wavy lines presenting a definite subdivision into cephalic and caudal portions and a clear separation into vermal and lateral contingents. The vermal division is formed of short sulci arranged in a rather aimless manner with a lateral portion which is more regular but still shows a somewhat sinuous type of folial division. None of the folia of lobulus 4 reach the periphery on account of the marked forward extension of lobulus C which hems in the lateral part of lobulus 4. Lobulus C presents three definite divisions in the folial pattern, corresponding to those of the arbor vitae. The most cephalic, lobulus C 3, is composed of a group of folia which disappear in the proximal portion of the fissura primaria, a very rudimentary lobulus simplex. The second portion, lobulus C 2, presents a distinct vermal distribution, the folia converging on a peduncle which is continued outward into what apparently is the sulcus intercruralis. The lateral folia of lobulus C 2 are apparently connected with the deep folia of the caudal portion of C 2 and continue outward as a sinuously arranged chain of lamellae which gradually turns forward, curving constantly inward, however, so that the peripheral terminations are in contact with the fissura primaria and, therefore, with the folia of lobulus 4 and of lobulus 2. These continue forward as crus 1 until they reach a point opposite the middle of lobulus 2 where the apex of the ansiform formation appears; crus 2 then develops as a group of folia continuing backward and inward, forming a sulcus intercruralis. In the middle of crus 2, a well defined folial rosette appears. The succeeding portion of crus 2 develops a peculiar method of implantation into the medullary substance which will be described later, the caudal folia of crus 2 apparently coming into connection with the lobulus C 2. Between lobuli C 2 and C 1, there appears a definite extrusion from the vermis of a folial rosette which is interposed between the termination of crus 2 and the lobulus paramedianus itself. The peduncle of this rosette is apparently connected with the submerged folia in the fissure between lobuli C 2 and C 1. Lobulus C 1 appears as a group of vermal folia from which there issues outward a peduncle on which develops a folial rosette which straightens out into a group of folia forming the lobulus paramedianus proper.

Lobulus B consists of a group of vermal folia, the cephalic half of which consists of narrow folia, and the caudal half of much wider folia. These folia converge on a peduncle which is directed outward and apparently is connected with the base of the lobulus parafloccularis. The lobulus parafloccularis is a remarkable structure

consisting of a series of much elongated folial rosettes, which closely succeed one another. At about the middle of the lobulus parafloccularis, there is one which is directed in an axis opposite to that assumed by the remainder. This group of folial rosettes continues outward along the course of crus 2 to the apex of the ansiform formation, where it turns back on itself still as a series of rosettes, and then terminates in a long drawn out uncus terminalis with a recurved tip of its own. This parafloccular formation is applied along the under and outer surface of the remainder of the posterior lobe. Lobulus A consists of a group of folia, at first short, which rapidly increase in width and then dwindle down to a small folium which is hidden in the depths of the fastigium. This is based on a peduncle which is continued outward in the general direction of the lobulus floccularis. The lobulus floccularis is a relatively simple structure consisting of a row of folia which expands into a folial rosette. It appears in the usual position between the peduncle of the cerebellum and the lobulus parafloccularis.

The implantation of the various lobes of the medullary substance presents the following arrangement: Lobulus 1 is implanted on the superior medullary velum as a lingua. Lobulus 2 has a distinct and independent implantation through a peduncle of its own. The implantation of lobulus 4 is hidden in the depths of the fissura primaria by the overgrowth of lobulus C. The ansiform formation, as far as the middle of crus 2, possesses a broad implantation in the medullary substance. The intermediate portion of crus 2 presents a peculiar lateral implantation in the development of a series of folial stalks, producing elongated rosettes which are continuous with two or more of the transverse folia of the middle portion of crus 2. Each of these folial groups or rosettes has a separate implantation into the medullary substance along the lateral margin of the paramedian and ansiform formations. The paraflocculus possesses a broad implantation for its serial group of rosettes ventral and lateral to the implantation of the remainder of the posterior lobe.

Physical characteristics of Phoca vitulina

The form of the seal shows a marked divergence from that of other carnivorous animals, directly dependent on its assumption of an aquatic habitat. The body is large and flat; the neck is relatively short but mobile, and the head is small with the eyes placed intermediately between the anterior and lateral positions. The eyes possess overlapping fields of vision and they are well conjugated. The tongue is moderately long and can be protruded to a considerable extent. The limbs are reduced to flippers for the sake of progression through the water, the fore limbs being capable of supporting the animal to a certain extent, but its progression on land is difficult and ungainly, being accomplished by a series of jumps. The posterior limbs are drawn out into flippers and are practically incorporated with the tail into a structure used only as a propulsive organ. The animal occupies an aquatic habitat in which its entire body is supported by the water, and when on land the ventral surface of the body rests on the ground, so that the limbs act little as a means of raising the body from the supporting surface, and are propulsive almost entirely and not supporting organs. The needs of this animal in equilibration, therefore, are relatively insignificant, while its requirements for coordinated activity of its entire axial musculature are enormously increased by the fact that

the mode or propulsion is fishlike, the body, hind limbs and tail acting as successively coordinated parts of a propulsive wave, while the fore limbs serve simply to direct the body and determine the position of the head near the surface of the water.

OTARIA GILLESPIEI (CALIFORNIAN SEA LION)

The arbor vitae of the California sea lion clearly indicates definite characteristics of the carnivora. It is more or less oval in outline. The fissura primaria appears in a position somewhat cephalad to the middle of the arbor vitae. It is chiefly

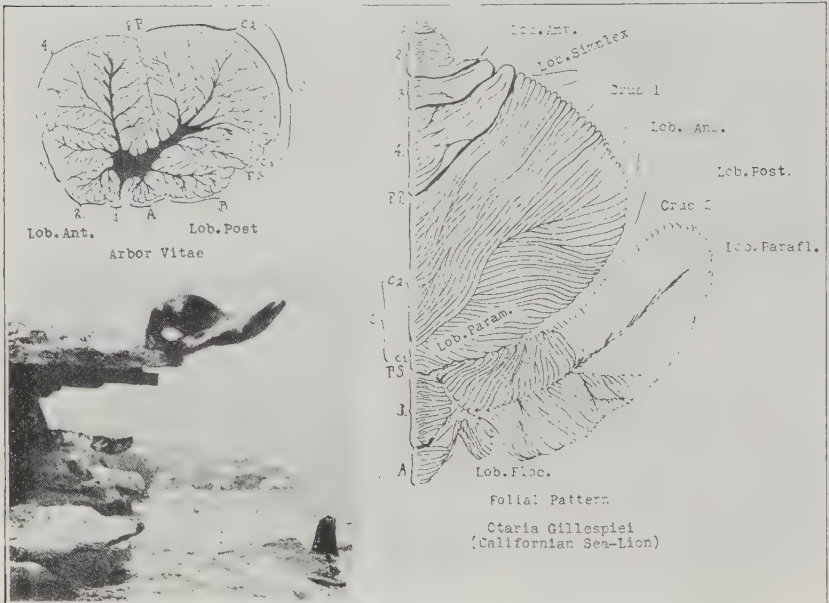


FIG. 22. *Otaria gillespiei* (California sea lion)

vertical turning somewhat forward in the depths of the fissure to approximate the medullary substance opposite the ventricular fastigium which is relatively narrow. The posterior lobe predominates in the median section, being more extensive than the anterior lobe. The fissura secunda appears in the usual position between lobuli B and C and lies in the general axis of the medullary substance of the posterior lobe. The medullary substance of the anterior lobe is collected in the center as a condensed mass of white matter which in passing into the posterior lobe becomes drawn out chiefly to form ray C. In general, the structure of the arbor vitae is rather delicate, the lobulation is rather extensive and the medullary rays are relatively light, except ray C, which is a heavy caudal extension of the medullary substance.

The medullary rays

Ray 1 appears as a lingular formation lying directly on the superior medullary velum. It resembles a tongue-like protrusion from the medullary substance of the anterior lobe. Ray 2 appears from the cephalic portion of the medullary substance as an independent stem which presents a number of lateral branches. Ray 3 arises from the cephalodorsal angle of the medullary substance as a long slender ray which proceeds forward giving off numerous subdivisions. Ray 4 is a relatively slender ray passing upward and giving off lateral branches. One of these is a relatively strong stem which proceeds forward and divides into two branches which are extensively subdivided. The caudal portion of ray 4 is heavier and gives off short but thick cephalic branches, while the caudal twigs are long and slender, and form the cephalic margin of the fissura primaria.

Ray C is the chief caudal continuation of the medullary substance, presenting a long drawn-out stalk which proceeds as a thick stem upward and backward. It appears as a thick, heavy ray which gives rise to a considerable number of branches, the most caudal of which have a peculiar arrangement as successive transverse laminae, corresponding to the folding under of the caudal portion of lobulus C 2 as seen in the folial pattern. Ray C 1 arises as a long slender branch, from the under surface of ray C and proceeds backward giving off lateral branches. Ray B arises from the lower and caudal angle of the medullary substance as a relatively well defined stalk giving off lateral branches and ending in a bifurcation. Ray A appears as a heavy stem arising from the under surface of the medullary substance immediately caudal to the fastigium, at once giving rise to two terminal branches.

The lobules

Lobulus 1 appears as a lingular group of folia arising from the superior medullary velum. Lobulus 2 consists of successive folia of small size, except the last which is coarser. Lobulus 3 is considerably larger than the preceding lobulus, presenting a number of surface folia. If lobulus 3 should be incorporated with either lobulus 2 or lobulus 4 it appears as more closely associated with the former than the latter. Lobulus 4 is considerably more extensive and presents two subdivisions. The cephalic group presents a rather extensive surface disposition and is subdivided into two folial groups. The caudal group does not possess so great a surface expression but presents a rather extensive development of folial groupings in the formation of the cephalic wall of the fissura primaria. Lobulus C 2 presents a greatly expanded surface, the folia being arranged in three definite subdivisions. The first group is formed by a fairly narrow set of folia, the second group is distinctly conical, the free surface being formed by an expanded spray of folia and the third group is arranged as a series of folial layers—long slender laminae which have few lateral branches, and indicate a rather extensive underfolding of the caudal lamellae of lobulus C 2. Lobulus C 1 appears as a slender lobulus with a small number of surface folia. Lobulus B has a considerable surface extent, each folium showing a subsidiary sulcus, the ventral folia being more highly developed than the dorsal lamellae. Lobulus A is noteworthy as it is considerably more condensed than usual.

The folial pattern of Otaria gillespiei

The fissura primaria is a well defined fissure appearing well forward in the folial pattern demarcating an anterior lobe which is markedly subservient in extent to the area of the posterior lobe. The latter has developed out of all proportion owing to the enormous expansion of the ansiform formation and the parafocculus. The fissura secunda appears separating lobulus B from lobulus C and is relatively short on account of the fact that the lobulus paramedianus is directly continuous with the vermal folia at this point. Lobulus 1, representing the lingula supported by the superior medullary velum, presents only a single folium subdivided laterally into three small serrations. Lobulus 2 presents a number of parallel folia transversely disposed, the cephalic being vermal while the caudal three present lateral extensions. The majority of these folia are subdivided in the midline. Lobulus 3 presents a fairly regular arrangement of the sulci in its vermal portion which become irregular in the hemisphere. The folial arrangement of lobulus 3 shows that it is more closely related to lobulus 2 than to lobulus 4. The first two sulci diverge from one another and come to an end, while the caudal three are joined together and fail to join the sulcus between lobuli 3 and 4, so that the lobulus which is subdivided into a considerable number of folia in the arbor vitae is reduced to a single thick folium at the periphery. Lobulus C consists of two separate subdivisions forming lobulus C 2 and lobulus C 1. Lobulus C 2 is much more extensive than lobulus C 1 and presents but little indication of a division into vermal and lateral portions. The sulci run, in general, a regular course, forming narrow folia which begin in the vermal region and extend outward for a variable distance. Lobulus C 2 presents five separate subdivisions, all of which begin as folia which run obliquely forward converging on a preceding sulcus. The successive folia then extend further and further outward until the caudal folia of each subdivision reaches the periphery. Except for this arrangement there is little indication of a differentiation between vermal and hemispherical portions. The folia forming the hemispherical portion are long and narrow and regularly arranged, and correspond with what may be termed crus 1 of the ansiform formation; they succeed a few folia which are arranged in a manner suggestive of the lobulus simplex. The lobulus ansiformis presents a slow gradual curve outward and an ill defined apex, following which the folia arrange themselves in a diminishing series returning toward the midline, the mesial terminations of the folia of crus 1 and crus 2, forming a definite sulcus intercruralis. The folial chain gradually diminishes in lateral extent, forming a lobulus paramedianus which becomes continuous with the vermal folia of lobulus C 1. The folia of lobulus C 1 continue to diminish, becoming relatively insignificant and are caudally limited by the fissura secunda.

Lobulus B presents a considerable group of folia, all of which are subdivided at the midline. These converge to form a folial rosette based on a peduncle which extends outward, apparently continuous with the middle of the parafoccular formation. The lobulus parafoccularis shows a definite connection with the caudal folia of the lobulus paramedianus, and continues outward as a regular folial chain of considerable lateral extent. When it reaches a point beyond the apex of the lobulus ansiformis it slowly returns on itself, the folia forming a definite interparafoccular

sulcus. This returning group of folia is interrupted at its midpoint by a marked irregularity in the arrangement of the folia owing to the formation of a group of ill defined and abortive rosettes. The regular arrangement returns, as the chain approaches the base of the lobulus parafocculus which is apparently continuous with the peduncle of lobulus B. Lobulus A consists of a series of diminishing vermal folia. The folia of lobulus A converge on a peduncle which is in apparent connection with a simple group of folia arranged as a single rosette which forms the lobulus floccularis, overshadowed by the parafoccular formation which lies over its base.

Lobuli 1, 2 and 3 present independent peduncular insertions into the medullary substance. The much expanded ansiform formation presents a wide single implantation, while the parafoccular formation is attached ventrally and laterally to the preceding lobulus.

Physical characteristics of Otaria gillespiei

The California sea lion presents a long, narrow, sinuous body, with an extended mobile neck, on which is supported a small head with a pointed nose. The eyes are situated in the anterior position, possess overlapping fields of vision and are well conjugated. The limbs are short, being capable of a limited and awkward use for locomotion. On land, the hind limbs are folded forward to support the rear of the body. The incorporation of the hind limbs and tail is not complete. The fore limbs present definite supportive characteristics, the distal portions of the limbs being converted, however, into flippers. The sea lion possesses a marked degree of agility and coordinative organization in its movements. The ability of the animal to catch articles thrown to it and to balance objects on its head is well known to those who have frequented any of the circuses. In fighting, the head of the sea lion is darted from side to side, and backward and forward, with great speed, and when the occasion appears the jaws close tenaciously on its adversaries. The tongue is of moderate size and is protrudable to a limited extent.

There is a considerable degree of unilateral independence in the fore limbs, and the animal is capable of a high degree of training and development. It possesses, in common with the seal, the characteristics acquired through its aquatic habitat, that is, the sinuous activity of the entire neck, body and limbs in progression through the water, the degree of axial coordination and integration being extreme, as evidenced by its remarkably smooth and graceful movements in water. While in the water it possesses a relatively simple degree of equilibratory needs; nevertheless, in its progress on land, where the limbs act as usual supports, there is a considerable need for this. It is capable of proceeding at a fair degree of speed on the surface of the ground.

ODOBAENUS (WALRUS)

The chief alteration in the arbor vitae of the walrus as compared with *Otaria* is the increase in size and thickness of the medullary outgrowths which present a much more outspoken and definite pattern in the arbor vitae. The general outline of the arbor vitae is not so nearly oval as in the other pinnepedia, there being

a considerable increase in the vertical depth of the section. There is an extensive increase in the richness of the subdivisions of the medullary rays and in the foliation, and the delicacy of organization found in *Otaria* has given place to a marked coarseness of ray and folium. The fissura primaria is situated more or less in the usual median plane of the arbor vitae showing a tendency to an oblique direction forward and downward at its termination as it attempts to approach the fastigium which is situated relatively far forward. The posterior lobe again exceeds the anterior lobe, chiefly through the caudal extension of rays C 1 and C 2. The fissura secunda is in about the usual position between lobuli B and C directed from

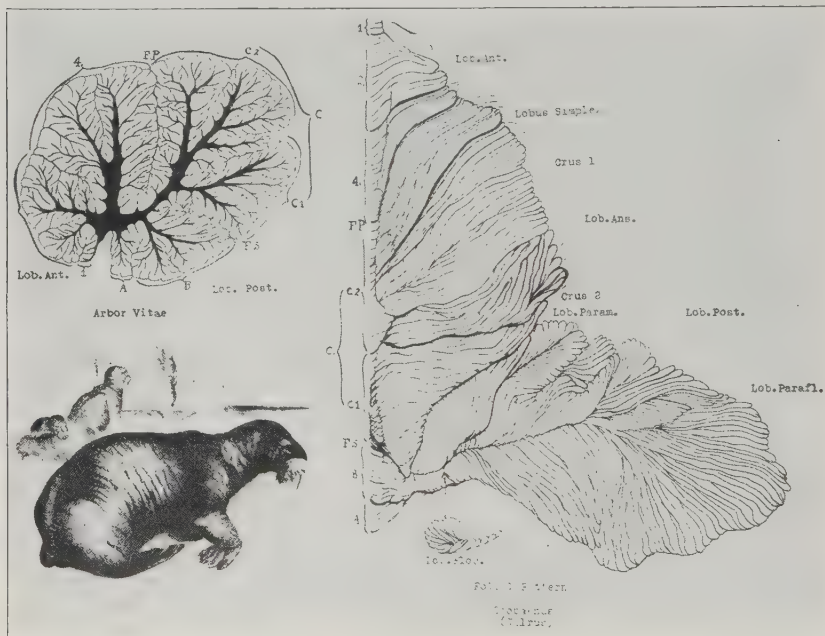


FIG. 23. *Odobaenus* (walrus)

before downward and backward. The ventricular fastigium is relatively advanced, fairly wide open, deep and based directly on the medullary substance. The medullary substance is disposed chiefly as a mass in the central core of the anterior lobe. It presents a marked extension vertically into ray 4. The medullary substance of the posterior lobe is disposed as a narrow caudal extension from the mass of white matter in the anterior lobe and is drawn out caudally and dorsally as a long crescentic ray C 2. There is only a small condensation of the medullary substance in the center of the posterior lobe.

The medullary rays

Ray 1 appears in the form of a lingula based directly on the superior medullary velum, from which arise a series of short, delicate branches. Ray 2 consists of a considerable extension forward of the anterior medullary substance as a thick stalk which immediately subdivides into two portions, a smaller ventral stem, and a much more extensive dorsal branch. The slender ventral branch proceeds downward and forward, giving off lateral twigs, and subdivides terminally. The dorsal stem is a thick, heavy branch proceeding directly forward and giving rise to a number of small slender ventral branches, and a series of much heavier branched dorsal stems, and terminates in a rather heavy bifurcation. Ray 4 is a large, heavy stalk which arises directly opposite the ventricular fastigium and proceeds almost vertically upward, giving off a number of simple cephalic branches. It then divides into two chief branches, the cephalic at once giving off a major subdivision which proceeds directly forward giving off a series of lateral shoots. The more vertical continuation of the cephalic branch of ray 4 proceeds upward and forward, giving off lateral branches and subdividing. The caudal primary division of ray 4 proceeds upward as a heavy stalk, with short, cephalic, and long slender caudal branches; the great majority of the latter terminate in a bifurcation and form the cephalic wall of the fissura primaria. Ray C appears as a direct continuation backward and upward of the posterior medullary substance. It is a relatively thick, curved stalk, giving off a major caudal subdivision, ray C 1. Ray C 2 continues upward as a heavy stem, dividing into cephalic and caudal divisions which subdivide a number of times, the latter much more extensively than the former producing a relatively complicated lobulus C 2. Ray C 1 proceeds directly backward, giving off a few side branches, and then divides into a dorsal more extensive and a ventral less extensive stem. These continue to give rise to a considerable number of lateral branches. Ray B arises at right angles to the general course of the posterior medullary substance as a relatively heavy stalk which divides into two primary branches. These two primary divisions give off numerous lateral shoots. Ray A arises as a thick stalk close to the fastigium, and gives off lateral branches.

The lobules

Lobulus 1 appears as a lingula composed of a number of folia which are supported directly by the superior medullary velum. Lobulus 2 is fairly complicated and quite characteristic. It is composed of two groups of folia. The ventral group is much less extensive and forms a conical sublobulus which presents further subdivision into two lamellar clusters. The dorsal sublobulus is rather more complicated, owing to the development of a series of fairly prominent dorsal stalks all of which give rise to a number of lateral twigs. The apex of this sublobulus is formed by the terminal divisions of the ray and is composed of two groups of laminae. Lobulus 4 is quite large and is subdivided into three folial subgroups by the division of the cephalic ray into a cephalic and a dorsal branch. The caudal division of the lobulus does not possess an extensive surface disposition, but is characteristic through the long series of caudal rays, each of which forms a folial group in the cephalic wall of the fissura primaria. Lobulus C is prominent and

rather complex. It is composed of two chief folial groups, lobuli C 2 and C 1. Lobulus C 2 presents a rather extensive surface disposition and can be divided into two groups of folia, the caudal being the larger and forming a protrusion at the dorsocaudal angle of the arbor vitae. The most caudal branch of C 2 is doubled and submerged, its lateral expansion being clearly recognizable in the folial pattern. Lobulus C 1 is much larger than that of *Otaria* and is divided into a dorsal group, which is further differentiated into two subgroups, and a ventral group, which shows the same type of division but not so extensively. This group of folia is entirely submerged from the surface by the mesial extension of the hemisphere. Lobulus B is also larger and is divided into two definite folial divisions both of which are composed of folial subgroups. Lobulus A is relatively simple and forms the caudal wall of the ventricular fastigium.

The folial pattern of Odobaenus

A considerable degree of difficulty is encountered in analyzing the folial pattern on account of the fact that the folia of the vermis are not directly continuous with those of the hemisphere. The presence of a definite, distinct paravermian fissure, through which it is difficult to trace the connection of the vermal and lateral portion of each folial group, adds to the complexity of the folial pattern. Another factor which makes it difficult to distinguish between the relative connections and identity of the various portions of the lateral hemisphere is that the groups of folia forming the lateral extension from the vermal region seem to fuse extensively. These areas of fusion are particularly marked at the approach of the folia to the vermal region and also at the periphery of the hemisphere. There cannot, therefore, be a clear and definite distinction between the folia forming the lateral lobular masses. The fissura primaria appears considerably cephalad to the middle of the folial pattern and continues sharply forward, then swings laterally into the hemisphere, demarcating a small anterior lobe and an enormously developed posterior lobe. The fissura secunda appears in the usual position between lobuli C and B, and is drawn sharply backward into a relatively long drawn-out elbow which apparently limits the paramedian formation and indicates the transition into the parafloccular development.

Lobulus 1 appears in the form of a lingula, based directly on the superior medullary velum. It consists of three small vermal folia. Lobulus 2 presents a definite division into a vermal and a lateral portion, many of the vermal sulci extending only for a short distance and tending to converge forward, thus cutting off a definite vermal from a distinct lateral portion, and establishing a paravermian sulcus. The lateral extensions increase from before backward, the group of folia in the most cephalic portion of lobulus 2 converging to form a single lateral folium which proceeds considerably outward from the midline. The second group of folia continues even further, being reduced in number as they approach the periphery until they consist of a single broad folium. The caudal portion of lobulus 2 presents a distinct division into a vermal part marked off by a paravermian furrow from a lateral portion which appears as a broad folium subdivided into three folia by the appearance of two lateral sulci. Lobulus 4 consists of a definite division into a vermal and a lateral portion, with the well defined development of a paravermian

sulcus. The vermal folia are relatively wide, the sulci separating them tending to run outward and then forward, disappearing in the paravermian sulcus. The folia of the lateral portion of the lobulus then appear as almost independent folia. They are much narrower, but about as numerous, so that their surface representation is much less than that of the lobulus in the arbor vitae. Lobulus C is divided into two definite portions, a more extensive cephalic and a less extensive caudal division, corresponding to lobuli C 2 and C 1. Lobulus C 2 consists of a chain of vermal lamellae which shows a tendency to widen and then narrow again toward the caudal portion of the lobulus. The connections with the hemispherical folia are again indistinct on account of the paramedian sulcus. The folia of the cephalic portion of lobulus C 2 are thin, well defined parallel lamellae which continue forward and outward, gradually decreasing in number. Toward the middle of the cephalic portion of lobulus C 2, a peculiar abortive rosette formation appears, which protrudes outward from the median line. This rosette apparently develops from a submerged folium seen in the arbor vitae in the depths of the fissure separating the two portions of lobulus C 2. The group of folia extending forward from the cephalic portion of lobulus C 2 are rather simply arranged and, appearing directly caudal to the fissura primarius, may correspond to the lobulus simplex. The folia succeeding the distinct sulcus which limits the lobulus simplex caudally begin to show some irregularity; the folia appear to run obliquely and the impression of a sulcus intercruralis is produced, thus indicating a rather poorly defined crus 1. The succeeding folia become still more irregular, particularly the terminal folia of lobulus C 2, which apparently correspond to the submerged folia seen in the arbor vitae between lobuli C 2 and C 1 that emerge from the sulcus and participate in the folial pattern. These lateral folia may represent crus 2. Toward the caudal termination of this group of folia the arrangement becomes much more irregular, and a rosette formation appears. The vermal folia of lobulus C 1 from a group submerged beneath the surface and out of sight unless the overhanging mesial termination of the folia forming the lateral expansion of C 1 is withdrawn from the midline. They then appear to be a group of small folia gradually increasing in size toward the caudal portion of the lobulus, forming a definite sulcus paramedianus. The folia disappear into this sulcus and then emerging turn mesially to form the overhanging margin which hides the vermal folia from sight. From this overhanging margin the folia pass outward, their lateral terminations turning forward. They decrease in width and form a long drawn-out termination. This entire formation is apparently the lobulus paramedianus and is limited by the lateral portion of the fissura secunda. Lobulus B appears as a fairly simple chain of lamellae, of considerable width and showing a tendency to swing forward at their lateral terminations with an indication of a rosette formation caudally. Lobulus B is continued laterally as a massive peduncle which flares out into the lobulus parafloccularis. This is a large and irregularly developed structure. It forms a considerable portion, at least a third—if not a half—of the cerebellum. It occupies the entire ventral aspect of the cerebellum. The folial chain begins at the termination of the lobulus paramedianus and continues outward as a series of folia which presents three large extensive rosette formations. Following this the folia become longer and longer, turn somewhat caudally at their tips and then are continued as a series of long, well defined folia, returning on the course they have already followed in the forma-

tion of the first series of folial groups. These gradually decrease in length and converge on the bare medullary stalk, which is of considerable size and is continuous with the base of the vermal portion of lobulus B. Lobulus A presents a relatively simple formation of a rosette, the cephalic folia being submerged beneath the surface within the depths of the fissure between lobuli A and B. From the peduncle of this rosette there is an ill defined line of connection extending outward beneath the root of the parafoccular formation to the lobulus floccularis which is hidden from sight by the root of lobulus parafoccularis. The flocculus is produced by a row of folia which gradually increase in size and form a definite terminal roset.

A single implantation appears for the first and second lobules, with a single small peduncle for the lateral portion of the fourth lobules, while the lobulus simplex and the rest of the lobulus ansiformis are inserted by a broad base into the medullary substance, lateral and ventral to which is applied the entire parafoccular formation.

Physical characteristics of Odoibaenus

The walrus is a large animal with a heavy body measuring from 10 to 12 feet in length, weighing a ton. It has four extremities, the fore limbs being similar to those of the sea lion, and the posterior limbs a compromise between those of the sea lion and the seal, possessing apparently less independence than those of the sea lion and more independence than those of the seal. The walrus can grasp and hold the prow of a boat with both fore flippers and drive his tusks through the planking. The tail is concealed between the hind limbs. The body is raised somewhat from the ground by the fore limbs, which act both as a means of progression and as a support. The head is small but heavy, the neck is short thick and massive and the eyes are placed laterally but turned forward so that the visual fields are overlapping. The eye movements are conjugated. The lips are mobile and can be retracted. The tongue is large and fairly mobile. The tusks are used for digging out mollusks and also to aid the animal in climbing. The walrus is thoroughly at home in the water and possesses extremely finished movements in swimming and playing in the water. The animal is incapable of extensive movement on land, the limbs being poorly differentiated as a means of progression on a solid medium. There is a slight degree of unilateral independence of the limbs.

CASTOR CANADENSIS (BEAVER)

The median section of the arbor vitae of the beaver presents a more or less oval outline, the long diameter of which is directed from before, backward and upward, the irregularity in outline being due to the development of lobulus C 2. The division into two lobes by the fissura primaria and the ventricular fastigium shows that the anterior lobe is of considerably less extent than the posterior lobe. The fissura primaria is directed from before backward and downward and does not directly approach the fastigium, which is broad and wide open. The disposition of the medullary substance is in the direction of the axis of the cerebellum, from before, obliquely backward and upward. The major portion of the medullary substance lies cephalad to the approach of the fissura primaria to the medullary substance, although, strictly speaking, a line drawn from the termination of the fissura primaria

to the limit of the fastigium would leave only a small proportion of the medullary substance in the anterior lobe. The medullary substance from which the cephalic stems arise is apparently more extensive than that from which the caudal rays arise, the posterior medullary substance being drawn out into a tail-like prolongation which forms the major portion of ray C 2. The fissura secunda is in the usual position between lobuli B and C and passes almost directly caudally from the medullary substance.

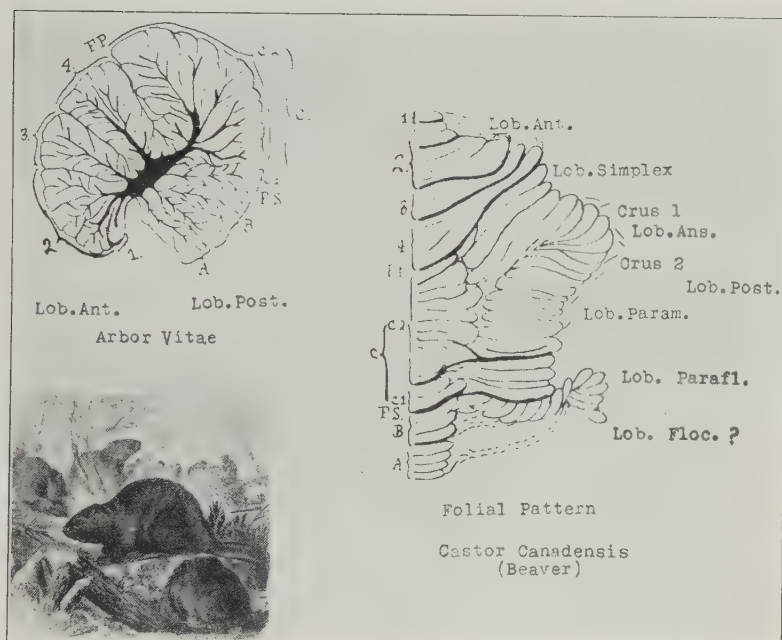


FIG. 24. *Castor canadensis* (beaver)

The medullary rays

Ray 1 arises as a single stem from the ventral aspect of the anterior medullary substance and is undivided. Ray 2 arises as a rather stout stem dividing into two groups of smaller branches, the dorsal ray giving rise to two divisions. Ray 3 is a long, slender ray directed upward and forward, giving off side branches and dividing at its summit. Ray 4 is a rather stout stem arising from about the midpoint of the medullary substance. It is directed upward and forward, presenting a single division and giving off a few small side branches. The division of the medullary rays of the posterior lobe presents a rather unusual arrangement which makes it difficult to determine exactly the identity of the various branches. A consideration, however, of the division of the arbor vitae, together with the folial

pattern, makes the identity of the individual branches relatively clear. Ray C really represents the caudal extremity of the medullary substance and gives off an independent ray C 1 which apparently arises without any direct connection with ray C 2. Ray C 2 is a direct caudal prolongation of the medullary substance, a relatively thick stem which divides into three or four caudal branches, the first two being almost horizontal, while the final divisions consist of a pair of slender, almost vertical branches, the cephalic branch giving off a group of branches which form the caudal wall of the fissura primaria. There is also connected with ray C 2 a rather prominent folium in the depths of the fissura primarius. Ray C 1 is given off from the main mass of the medullary substance opposite the depths of the fissura primaria. It continues back as a simple stalk, giving off side branches. Ray B arises in front or just below the origin of C 1 as a slender stem which immediately divides into two branches that give off numerous twigs. Ray A arises close to the fastigium as a slender branch directed downward and backward, giving off several smaller branches.

The lobules

Lobulus 1 appears as a single simple folium which forms the cephalic wall of the fastigium. Lobulus 2 is of fair size and subdivided into a smaller ventral and a larger dorsal portion. These are simply arranged and consist of broad folia without much secondary division. Lobulus 3 is narrow, consisting of two surface folia with one small subdivision. Lobulus 4 is somewhat more extensive, presenting on the surface two chief folia which are subdivided by short fulci. Lobulus C presents two portions which are distinctly different in their folial arrangement. Lobulus C 2 is a large extensive group of folia. It is subdivided into a considerable number of subsidiary folial groups. The first of these presents a number of folia in the depths of the fissura primaria while caudally it is much reduced. There then succeed three groups of folia which approach the horizontal plane, each folium possessing a medullary ray which arises independently from ray C 2. Lobulus C 1 is a much reduced narrow lobulus and presents on the surface only two small folia. Lobulus B presents a definite division into two portions which possess a rather simple folial arrangement. Lobulus A is a simple folial group.

*The folial pattern of *Castor canadensis**

The fissura primaria arises at a point somewhat cephalad to the middle of the folial pattern and proceeds in a simple curved fashion forward and outward to the periphery. The fissura secunda is a definite fissure in the folial pattern of the beaver and supplies an unmistakable separation between lobuli B and C and the lobulus parafoveolaris and the lobulus paramedianus. It appears in its usual position between lobuli C and B and is continued directly into the hemisphere on account of the fact that the folia of the lobulus paramedianus are continuous with the folia of the vermis in this portion of the posterior lobe. Lobulus 1 consists of a single vermal folium. Lobulus 2 is formed by a cephalic group of vermal folia and a caudal group made up of two wide folia which present lateral extensions and are subdivided for the most of their extent into four minor folia, reduced at the periphery, however, to two folia. Lobulus 3 arises as a divided folium which,

however, is continued as a long narrow lamina. Lobulus 4 presents definite vermal divisions into four small folia which consolidate by the disappearance of the sulci into one long lamella. Lobulus C is divided into a complicated cephalic and a simple caudal portion. The cephalic division is lobulus C 2 and consists of parts representing vermal and lateral subdivisions. The vermal folia consist of a straight series of folia which are rather irregular in size, shape and lateral extent. The caudal group presents the formation of a rosette. The lateral folial extensions are separated from the vermal portions by a distinct paramedian groove except the most caudal folia, in which the vermal and lateral portions are continuous. The lateral chain consists of a few simple folia immediately caudal to the fissura primarius, extending outward to the periphery as a lobulus simplex. Following these folia, there ensues a well defined lobulus ansiformis, with a rather broad poorly differentiated group of folia passing over into a definite crus 1 which turns on itself in the usual manner and returns as crus 2, with a definite intercrural sulcus. At the point where crus 2 again resumes contact with the vermal group, the folia turn backward as the lobulus paramedianus which terminates in two rather broad folia that are continuous with extensions from the most caudal vermal folia of lobulus C 2. Lobulus C 1 consists of two well defined vermal folia which are continuous with a group of four folia that pass outward and become the caudal folia of the lobulus paramedianus, the more cephalic of which are connected with the submerged folium seen in the arbor in the depths of the fissure separating lobuli C 2 and C 1. The paramedian formation is bounded caudally by the fissura secunda. Lobulus B presents three simple vermal folia, the most cephalic of which are directly continuous with the end of the parafloccular formation. The paramedian formation is continuous in the depths of the fissura secunda with the lobulus parafloccularis by a group of diminishing folia which converge downward toward the root of the parafloccular formation. The paraflocculus itself is a relatively simple structure consisting of a series of folia which continue outward in the direction at right angles to the axis of the paramedian folia and then terminate as a rather rudimentary folial cluster. Lobulus A consists of a simple group of vermal folia which converge on a peduncle which is continuous outward in the general direction of the lobulus floccularis. The lobulus floccularis is extremely poorly developed, the only indication which can be found of its existence being a single large folium which appears at the termination of the lobulus parafloccularis.

The insertion of the various lobules into the medullary substance shows that the first and second lobules are inserted together by a single peduncle. The third and fourth lobules show a similar arrangement, sharing a peduncle between them. The lobulus simplex, lobulus ansiformis and lobulus paramedianus are all inserted by means of a broad base into the medullary substance, while the parafloccular formation in its free portion appears ventral to, and somewhat in front of, the apex of the lobulus ansiformis.

Physical characteristics of Castor canadensis

The beaver is a terrestrial animal, thoroughly at home in the water, being capable of a more perfect means of progression in the water than on land. It can dive and swim as easily and gracefully as a seal. The body of the animal is

fairly heavy, with a short neck and a narrow head; the eyes are situated well on the lateral aspect, the fields of vision overlapping to only a slight degree and possessing but little conjugated movement. The tongue is small, short and rounded and is not protrudable to any extent. The limbs are short and the hind feet are much larger than the fore feet, the body of the animal largely resting on the ground when it is quiet. It has a sort of lumbering walk-trot or gallop, whereas it swims with remarkable speed and agility. It presents a well marked broad flat tail, about 10 inches in length and covered with scales, which is capable of adding materially to its speed in traversing the water. The fore paws are short and broad, with a well developed thumb, and they are capable of a marked degree of unilateral independence, the paw grasping and holding objects such as saplings as the beaver bites the stem.

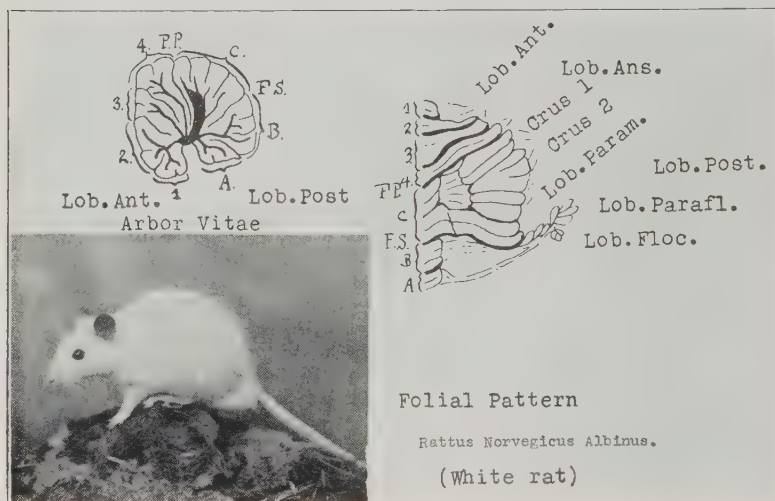


FIG. 25. *Rattus norvegicus albinus* (white rat)

RATTUS NORVEGICUS ALBINUS (WHITE RAT)

The outline of the arbor vitae of the white rat presents a rather conical form, lobulus 4 forming the summit. The fissura primaria is situated a little cephalad to the middle of the arbor vitae, almost directly opposite the ventricular fastigium which reaches the medullary substance and is relatively wide. The arbor vitae is divided by the fissura primaria and the ventricular fastigium into anterior and posterior lobes, the anterior lobe being somewhat smaller than the posterior lobe. The fissura secunda separates the posterior lobe into two almost equal halves, being somewhat above the midline of the posterior lobe. It is situated in the usual position between lobuli B and C.

The medullary substance of the arbor vitae presents a condensation in the

center of the cerebellum which is continued forward as a small nubbin into the anterior lobe from which the medullary branches arise. The medullary substance of the posterior lobe presents a small condensation from which arise the thick, heavy ray C and the slender rays B and A.

The medullary rays

Ray 1 arises in conjunction with ray 2 from a common stem which springs forward from the medullary substance as a thin stalk. It does not belong, however, to lobulus 2, for an examination of the folial pattern shows that the two are separate and distinct in their foliation. Ray 2 consists of two simple branches, which diverge from one another. Ray 3 appears as a definite independent slender stem, arising from the dorsal aspect of the anterior medullary substance. It proceeds upward and forward in a somewhat arched manner, has no side branches and terminates in a simple division. Ray 4 is similar in its origin and is also devoid of lateral stems until near its summit, where it gives off a few branches. Ray C is a thick, heavy stem appearing as a massive offshoot from the nubbin which forms the posterior medullary substance. It arises from the dorsal and caudal aspect of the posterior medullary substance and gives off thin and undivided caudal branches. There are no cephalic branches. Ray B arises as a simple continuation backward of the medullary substance and divides into two branches. Ray A arises as a simple stem, almost by a common origin with ray B, from the ventral surface of the posterior medullary substance.

The lobules

Lobulus 1 is subdivided by a shallow sulcus which forms two rather broad folia. Lobulus 2 also presents two broad laminae corresponding with the terminal division of ray 2. Lobulus 3 is a simple, narrow lobulus possessing a median division. Lobulus 4 is simply arranged, presenting only two surface folia. Lobulus C is much more extensive, although rather undifferentiated, presenting four fairly broad surface lamellae. Lobulus B presents three folia, and lobulus A, two folia.

*The folial pattern of *Rattus norvegicus albinus**

The folial pattern of the albino rat is simple and presents a division into a small anterior lobe and a considerably larger posterior lobe. The fissura primaria is somewhat cephalad of the middle of the pattern, passing almost directly outward and forward. The fissura secunda appears in its usual position between lobuli B and C and continues outward, terminating the chain of folia forming the lobulus paramedianus. Lobulus 1 presents a simple arrangement consisting of one vernal folium. Lobulus 2 presents a median subdivision but terminates as a simple folium which has a distinct extension into the hemisphere. Lobulus 3 has a similar disposition with a larger caudal division being reduced laterally to a single folium. Lobulus 4 presents a narrow folium which is subdivided in the greater part of its extent by a sulcus, but terminates as a single folium which has, however, a considerable lateral extent. Lobulus C presents a cephalic and a caudal portion. The cephalic portion represents the usual lobulus C 2 and is confined chiefly to the

vermis but is connected in its cephalic part by a thin folium with the lateral portion of the lobulus. A distinct paramedian sulcus develops, in the depths of which can be found a definite connection between the folia of the vermis and of the lateral hemisphere. The lateral folia appear as a simple chain which continues caudally as a poorly defined lobulus ansiformis with only a suggestion of crus 1 and crus 2. Succeeding crus 2 are two simple folia forming the cephalic portion of the lobulus paramedianus, caudal to which are two much wider folia which correspond to the folia usually recognized as the lateral portion of C 1 and are directly continuous with the caudal vermal folia of lobulus C 1. Lobulus B presents a cephalic folium subdivided laterally, and a caudal single folium. This forms a rosette the peduncle of which is apparently continuous with the parafloccular formation. The para-floccular formation is simple in arrangement, consisting of only a few small folia, directly succeeding the folia of the paramedian formation. It continues outward into a rosette. Lobulus A presents a single folium, subdivided partially by a median sulcus. Its peduncle extends toward the lobulus floccularis which is made up of a tiny rosette consisting of three small folia.

Lobulus 1 and lobulus 2 present a common peduncular implantation into the medullary substance. Lobulus 3 and lobulus 4 have independent attachments. The ansiform and paramedian formations have a common broad implantation, lateral and ventral to which is situated the parafloccular insertion.

Physical characteristics of Rattus norvegicus albinus

The white rat has the typical body form of a small rodent; the legs are rather slender and of moderate length. The neck is relatively short, and the head is long and pointed. The eyes are situated in the lateral position and possess but little overlapping in the visual fields. The eye movements are rather limited and do not present much conjugation. The ears are well developed. The head is freely movable. The tail is long and slender and aids the animal somewhat in its rapid movements. The activity of the animal is rather simple. It is agile and speedy, and possesses a good deal of celerity. The anterior and posterior extremities present a considerable degree of unilateral independence. The fore limbs are independent, the animal being able to sit on its haunches, hold its food in its fore paws and handle it almost as if the fore paws were hands.

CAVIA PORCELLUS (GUINEA-PIG)

The arbor vitae of the guinea-pig presents a more or less rounded outline. The fissura primaria is almost in the midline, descending perpendicularly toward the summit of the fastigium, these two structures dividing the arbor vitae into practically equivalent anterior and posterior lobes. The ventricular fastigium is prominent and wide open, and is surmounted by the medullary substance of the anterior and posterior lobes. The fissura secunda appears in its usual position between lobuli B and C, considerably above the midline of the posterior lobe, directed from before backward and upward. The medullary substance lies in the center of the cerebellum forming the roof of the ventricular fastigium, its major portion lying in the anterior lobe. There is a constriction at the point of approach of the fissura primaria to the fastigium with a downwardly curved prolongation into the posterior lobe.

The medullary rays

Ray 1 is a simple ray extending forward from the downturned extremity of the anterior medullary substance. Ray 2 arises independently from the cephalic aspect of the medullary substance and divides simply. Ray 3 arises as a single ray from the dorsal and cephalic aspect of the medullary substance and divides at its summit into two simple branches. Ray 4 arises from the dorsal aspect of the anterior medullary substance and proceeds somewhat forward and upward, giving off simple branches and bifurcating at its termination. Ray C is a slender stem arising from the dorsal aspect of the caudal termination of the posterior medullary

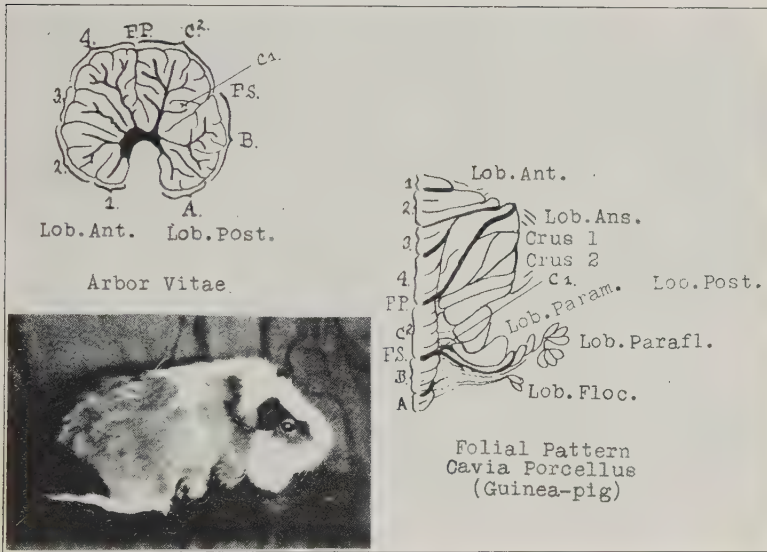


FIG. 26. *Cavia porcellus* (guinea-pig)

substance. It is directed upward and gives off a cephalic, a caudal and three terminal branches. The caudal branch, arising opposite the cephalic stem, forms a folium in the depths of the fissura secunda, which extends outward into the lobulus paramedianus and is ray C 1. Ray B arises as a direct continuation caudally of the posterior medullary substance. It is a single stem which undergoes a simple degree of subdivision at its termination. Ray A proceeds downward from the caudal extremity of the posterior medullary substance as a simple stem which undergoes one subdivision at its summit.

The lobules

Lobulus 1 consists of a single folium. Lobulus 2 is composed of three simple folia of relatively large size. Lobulus 3 is narrow and presents a subdivision into

two separate folia. Lobulus 4 is a simple conical lobulus presenting three surface folia and a few rudimentary folia in the cephalic margin of the fissura primaria. Lobulus C shows a simple process of division into four surface folia which forms lobulus C 2 and a submerged folium in the depths of the fissura secunda which is continuous with a paramedian folium and represents lobulus C 1. Lobulus B consists of two portions, a larger dorsal and a smaller ventral division, and presents four definite folia. Lobulus A is relatively simple and consists of a single divided folium.

The folial pattern of Cavia porcellus

The folial pattern of the guinea-pig presents the usual division into anterior and posterior lobes by the fissura primaria, the former being simpler and much less extensive than the latter. The origin of the fissura primaria takes place at the middle of the folial pattern, and proceeds outward, forward and then outward again to the periphery. The fissura secunda appears in the usual position between lobuli B and C and is continued outward, caudally limiting a folium which extends from the depths of the fissura secunda outward to incorporate itself in the lobulus paramedianus. Lobulus 1 is a simple vermal folium. Lobulus 2 presents a pair of folia, the cephalic of which is subdivided into the vermal region. The lateral portion is undivided and presents distinct evidence of participating in the formation of the hemisphere. The caudal folium is undivided and extends uninterruptedly from the midline to the periphery. Lobulus 3 is confined entirely to the vermis, the limiting sulcus running forward and participating in the formation of a well defined paravermian sulcus. The lobulus ends in the depths of the fissure between lobulus 2 and lobulus 4. Lobulus 4 consists of three vermal folia which are separated from the lateral portion of the lobulus by a distinct paravermian sulcus. Lobulus 4 is continued outward into the lateral mass at a single, wide folium which assumes considerable proportions and then is reduced to a narrow lamina at the periphery. Lobulus C presents a definite division into vermal and lateral portions. The vermal portion of lobulus C 2 consists of two relatively wide folia and one narrow one, forming a rosette which, by means of a peduncle, is continued outward into the hemisphere. The first folium of the lateral portion of lobulus C is disposed transversely and is limited to a small triangular distribution at the cephalic extremity of the lobulus, limited by the fissura primarius in front. The next three folia are arranged as a poorly defined lobulus ansiformis forming crus 1 and crus 2. Succeeding this peculiar folial arrangement, the lobulus paramedianus appears first as two wide folia, and then two small folia which form the contracted portion of the lobulus paramedianus. The last folium but one of the lobulus paramedianus is a rather large lamina, continuous with part of the peduncle of lobulus C, while the terminal folium of the lobulus paramedianus is continuous in the depths of the fissura secunda with the submerged folium marked C 1 in the arbor vitae. Lobulus B consists of three small vermal folia, the caudal two of which show subdivision. These form a simple rosette the peduncle of which is directed outward parallel with the fissura secunda, apparently ending at the base of the parafloccular formation. The lobulus parafloccularis is a simple group of folia continuing the lateral twist of the termination of the lobulus paramedianus and being applied to the under and outer surface of the lobulus paramedianus and the

ansiform formation. It terminates in a simple rosette formed by three or four small folia, which is again succeeded by another roset of about the same proportions. Lobulus A consists of a single folium, subdivided in the median line, which is continued outward in the general direction of the lobulus floccularis by means of a peduncle. The lobulus floccularis consists of only two small folia lying in the usual position of the floccular formation, between the peduncle of the cerebellum and the lobulus parafloccularis.

The entire anterior lobe has a common implantation in the medullary substance. The posterior lobe has an implantation for the ansiform and paramedian formation which is separate from that of the lobulus parafloccularis.

Physical characteristics of Cavia porcellus

The guinea-pig is a relatively small animal. Its head is large, with the eyes situated laterally, presenting little overlapping in the visual fields and but little mobility. The tongue is small. The neck is short. The body is round and elongated and the limbs are short. The tail is rudimentary. The guinea-pig possesses a fair degree of agility and speed. It can sit upright and use its fore limbs with a considerable degree of unilateral independence.

DASYPROCTA AGUTI (AGOUTI)

The median section of the arbor vitae of the agouti presents a more or less quadrilateral appearance, the vertical diameter somewhat in excess of the horizontal, owing to the dorsal development of lobulus 4. The fissura primaria is caudal to the middle of the arbor vitae and proceeds from behind forward and downward toward the ventricular fastigium, which appears at about the middle of the ventral aspect of the cerebellum. The fastigium is narrow and closed in. The division into two lobes by the fissura primaria and the ventricular fastigium shows that the anterior lobe predominates somewhat. The medullary substance is condensed in the center of the cerebellum, there being no clear demarcation between that belonging to the anterior lobe and that of the posterior lobe. The part which lies in the anterior lobe, according to the approximation of the fissura primaria with the fastigium, considerably exceeds that lying within the confines of the posterior lobe and is disposed as a rather bulbous protrusion into the anterior lobe, while the medullary substance of the posterior lobe appears as a rather conical protrusion into the posterior lobe.

The medullary rays

Ray 1 arises as a lingular formation on the superior medullary velum. Ray 2 appears as a group of stalks arising from the extension forward of the medullary substance consisting of three small branches; the first, a single unbranched stem, the second with a terminal bifurcation, and the third arising as a single stem which by bifurcation produces two definite subsidiary branches. Ray 3 arises independently from the dorsal aspect of the anterior medullary substance and proceeds in an arched manner, upward and then forward, giving off a few lateral branches and bifurcates. Ray 4 arises directly perpendicular, opposite the ventricular fastigium,

as a relatively heavy stalk, giving off small and relatively larger lateral branches. Ray C arises as a single stalk which is concerned chiefly in the foliation of lobulus C 2. It proceeds directly backward and upward, and then turns still more upward, giving off simple side branches. It presents little secondary branching. In the depths of the fissura secunda is found one submerged folium which is continuous laterally in the folial pattern with the last folium of the lobulus paramedianus and represents lobulus C 1. Ray B arises as a thick, heavy extension directly backward from the medullary substance. It gives off a few side branches and then divides into two chief subdivisions which give off lateral shoots and form terminal divisions. Ray A is a simple stalk from the ventral aspect of the medullary substance forming the caudal limit of the ventricular fastigium.

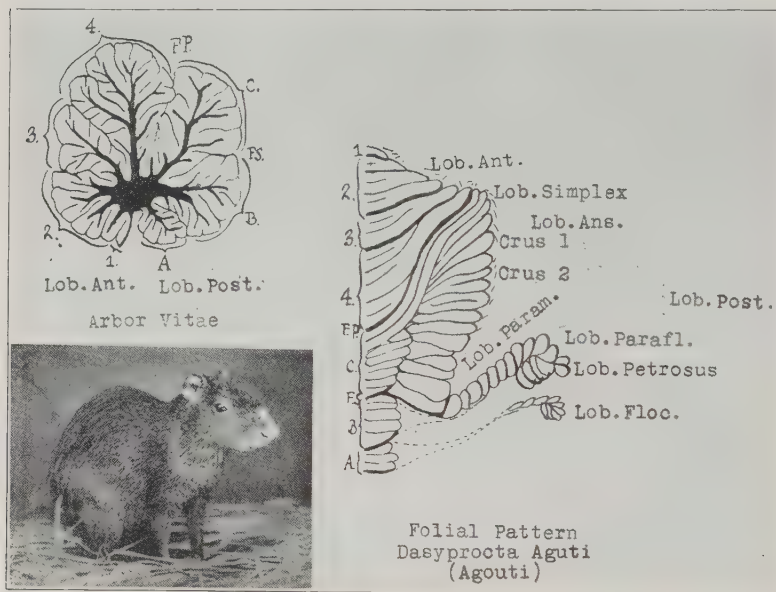


FIG. 27. *Dasyprocta aguti* (agouti)

The lobules

Lobulus 1 corresponds with the lingular formation, there being a small deposit of cortical substance on the superior medullary velum. Lobulus 2 is subdivided into three definite portions, the first presenting an undivided folium, the second a simple division and the third a much more definite separation into two folial groups. Lobulus 3 is a simple lobulus with two folia; it presents a definite indentation corresponding with the position of the midbrain collicular plate. Lobulus 4 forms the summit of the anterior lobe and presents a rather extensive serial succession of simple folia on its surface. Lobulus C 2 is small and is formed by four or five

simple folia. A single submerged folium in the depths of the fissura secunda which continues outward into the lobulus paramedianus represents lobulus C 1. Lobulus B shows a subdivision into two portions, a larger dorsal and a smaller ventral division, the former presenting three folia and the latter, two. Lobulus A presents a simple arrangement of consecutive folia.

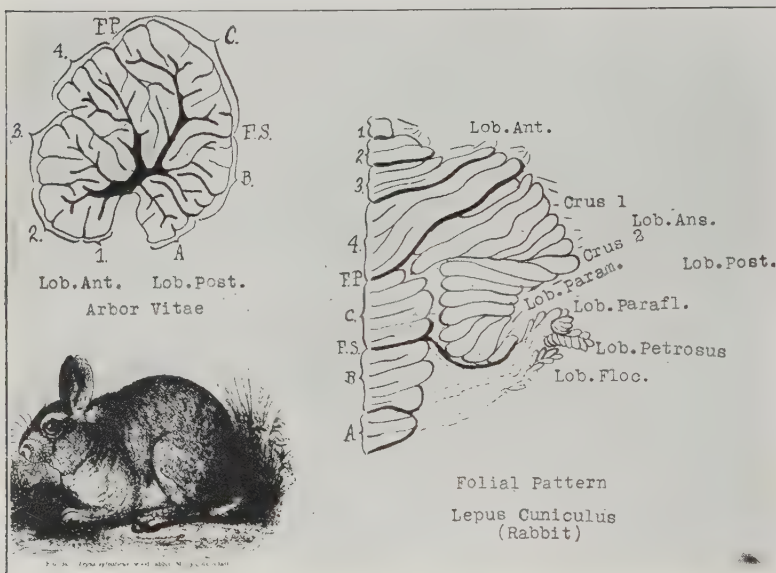
The folial pattern of Dasyprocta aguti

The position of the fissura primaria is somewhat caudal to the middle of the folial pattern and presents a sinuous course forward and outward to divide the cerebellum into anterior and posterior lobes. The fissura secunda is well defined, appearing between lobuli B and C, and forms the caudal limit of the lobulus paramedianus. Lobulus 1 consists of a single vermal folium lodged on the superior medullary vellum. Lobulus 2 presents three subdivisions which are indicated in the folial pattern as the folia gradually increase in length, extending outward into the hemisphere, and also presenting vermal subdivisions. Lobulus 3 is a simple lobulus consisting of three small folia which become reduced laterally to a single folium. Lobulus 4 presents a considerable distribution in the midline, but is rapidly reduced to a single folium which extends outward into the lateral mass. It shows a definite vermal division with small, short, vermal sulci. Lobulus C 2 presents a division into two portions. The cephalic subdivision shows a pair of simple striplike folia which run directly parallel with the fissura primaria from the midline to the lateral periphery, representing a well defined lobulus simplex. The remainder of lobulus C 2 is divided into definite vermal and lateral portions. The vermal portion consists of a series of diminishing folia. The lateral portion presents a chain of folia directly following the lobulus simplex forming a poorly defined lobulus ansiformis without any clear differentiation into crus 1 and crus 2. There is a direct continuation backward of crus 2 into the lobulus paramedianus, without any definite line of demarcation. These folia are rather broad and large, are regularly arranged and continued backward. The last folium which is a direct continuation outward of the submerged folium in the fissura secunda represents lobulus C 1. Lobulus B consists of a folial rosette continued outward as a peduncle toward the base of the lobulus parafoccularis. The lobulus parafoccularis follows immediately on the terminal folium of the lobulus paramedianus; the chain of folia extends forward to the region of the poorly defined lobulus ansiformis where it terminates in a distinct rosette with a protrusion outward of two folia which form a fairly well defined lobulus petrosus. This is then continued backward into a short uncus terminalis. Lobulus A consists of a few folia in the form of a rosette, which is connected by a peduncle with the termination of the lobulus floccularis. The lobulus floccularis consists of a simple rosette formation, with a tail formed by a few folia situated between the peduncle of the cerebellum and the parafoccular formation.

The implantation of the lobules into the medullary substance follows a relatively simple arrangement. The first lobulus and one half of the second lobulus are implanted together. The second half of the second lobulus and the third lobulus have a common peduncle. The tapering extremity of the fourth lobulus has an independent attachment, while the posterior lobe has a broad implantation lobulus C medially, and the lobulus parafoccularis laterally.

Physical characteristics of Dasyprocta aguti

The agouti is a rather small rodent; it has four limbs which are of fair length and quite slender, the body being raised considerably off the ground. The hind limbs are somewhat longer and more powerful than the fore limbs. The neck is well formed, and the head is small, with the eyes placed distinctly in the lateral position and possessing but little mobility. It is swift and nimble in its movements. It is a ground dwelling rodent, with hooflike claws. Its method of progression is walking and hopping, the propulsion being supplied chiefly by the longer and more powerful hind legs.

FIG. 28. *Lepus cuniculus* (rabbit)

LEPUS CUNICULUS (RABBIT)

The arbor vitae of the rabbit presents a distinctly conical form. The ventral portions of the anterior and posterior lobes constitute the base, and the apex is formed by the summit of lobulus C which presents the formation termed by Bolk, the lobulus impendens. The median section is divided into about equivalent anterior and posterior lobes by the fissura primaria which extends in a curved direction backward, downward and slightly forward as it approaches the ventricular fastigium which is situated somewhat in advance of the termination of the fissura primaria and is wide open. The fissura secunda appears rather high up in the posterior lobe, dividing the lobe into almost equal halves.

The medullary substance is arranged in a rather irregular manner without any definite condensation and extending forward into lobulus 2 and upward into lobuli 4 and C.

The medullary rays

Ray 1 arises as a single undivided stem from the ventral surface of the anterior medullary substance. Ray 2 appears as the direct forward prolongation of the medullary substance, presenting a few simple branches. Ray 3 arises apparently independently from the dorsal aspect of the anterior medullary substance and gives off a number of side branches. Ray 4 continues upward and then forward, first as a fairly heavy stem, then as a slender bifurcated stalk, giving off a small number of side branches. Ray C is a long, slender stalk, arising from the insignificant posterior medullary substance; it proceeds backward, then upward and finally distinctly forward, so as partially to overhang lobulus 4. It gives off a few branches and then divides into a bifurcation which forms the summit of the lobulus. Ray B arises as a single stem from the junction of ray C and the posterior medullary substance, and then divides into two simple branches. Ray A arises as a single simple stalk from the ventral surface of the posterior medullary substance, close to the ventricular fastigium, and gives rise to a few lateral branches.

The lobules

The lobulation of the arbor vitae shows a simple single folium as lobulus 1, a double folium as lobulus 2 and three folia forming lobulus 3. The impression of the mesencephalic collicular plate is clearly seen between lobuli 3 and 4. Lobulus 4 consists of two fairly large folia which are subdivided into four subsidiary lamellae. Lobulus C occupies a relatively large amount of the surface of the posterior lobe, presenting wide, simple, undivided folia. Lobulus B is divided into two portions consisting of three and two folia, respectively, while lobulus A presents two surface folia and one in the depths of the fastigium.

*The folial pattern of *Lepus cuniculus**

The folial pattern shows a distinct division into anterior and posterior lobes through the fissura primaria which appears somewhat cephalad to the middle of the pattern and proceeds outward and forward in rather a wavy course. The anterior lobe is considerably less in extent than the posterior lobe. The fissura secunda appears in its usual position between lobuli C and B, and presents a definite continuation outward to form the caudal limit of the lobulus paramedianus. Lobulus 1 consists of a single vermal folium. Lobulus 2 presents two simple folia which are continued outward into the hemisphere. Lobulus 3 presents two folia which are subdivided by short sulci, the caudal folium being considerably more extensive than the cephalic folium. Lobulus 4 consists of two chief folia which are subdivided into five smaller folia in the vermis region but are reduced, by the failure of the sulci to continue outward into the hemisphere, to two sinuous folia which reach the periphery. The posterior lobe is divided by a definite paramedian sulcus into vermal and lateral portions. The vermal portion of lobulus C consists of four chief folia, the caudal two of which are subdivided by short sulci. These

are arranged in a rosette which is continuous with a wide peduncle, which, in turn, is continuous in the depths of the paramedian fissure with the ansiform and paramedian formations. There is no definite arrangement of a lobulus simplex, the folia of the lateral mass not being continuous with the vermal folia. The lateral folia are arranged in a successively diminishing series, forming a definite crus 1 which continues outward to an apex and then returns on itself by means of two or three long folia, the mesial extremities of which, in contact with the mesial extremities of the folia of crus 1, form a well defined sulcus intercruralis. Following crus 2, the paramedian formation appears as a chain of simple lamellae, which, in the region of the caudal portion of lobulus C, turns outward to be limited by the extension of the fissura secunda. Lobulus B consist of three rather large folia which are divided in the vermal region by short sulci. They converge on a peduncle which is continued outward to the beginning of the lobulus parafloccularis. The lobulus parafloccularis is a simple structure, the lamellar chain being directly continuous with the caudal folia of the lobulus paramedianus. It is continued forward and outward and terminates in a rosette with a definite extension laterally, forming a lobulus petrosus and a rudimentary uncus terminalis. Lobulus A consists of a small group of folia arising from a peduncle which is continued outward in the general direction of the lobulus floccularis. The lobulus floccularis appears as a simple rosette terminating in a short chain of floccular folia situated in the usual position between the peduncle of the cerebellum and the parafloccular formation.

The various lobules show definite medullary insertions. Lobuli 1 and 2 are implanted by means of a single peduncle. Lobuli 3 and 4 present independent peduncles, while the ansiform and paramedian formations are inserted by means of a simple, wide base into the medullary substance. The parafloccular formation is inserted ventrally and laterally to the paramedian formation.

The physical characteristics of Lepus cuniculus

The rabbit is a quick, active, four-legged animal, with a moderate sized body supported by short forelimbs and long hind limbs. The neck is short; the head is small, with large ears, and the eyes are situated in the lateral position and have but little mobility. The activity of the animal is, at times, remarkable. It is quick, lithe and energetic. The hind limbs are used chiefly in driving the animal forward in long leaps, the fore limbs being largely for the means of directing its progression. The tail is small, rudimentary and insignificant. The animal is capable of rising on its hind legs and balancing itself successfully in its effort to look around and also to search for food. In this position, with the fore limbs freed from the necessity of station in locomotion, it is capable of a considerable degree of unilateral independence, holding and turning its food in its paws as if they were hands.

MEGACHIROPTERA-PTEROPUS (FLYING FOX OR FRUIT BAT)

The arbor vitae of the fruit bat presents a more or less quadrilateral form, with a distinct prolongation of the ventrocaudal angle into a caudal extension. The fissura primaria is situated almost in a vertical line and placed directly over the

ventricular fastigium, which is relatively narrow. The presence of the fissura primaria and the fastigium divides the arbor vitae into anterior and posterior lobes, the anterior being considerably smaller than the posterior lobe. The fissura secunda appears a little above the plane of the medullary substance, in the lower half of the arbor vitae, and is directed from before somewhat backward and upward. It separates lobuli B and C.

The medullary substance is disposed as a simple condensation in the lower portion of the arbor vitae, a small more or less elongated, oval structure from which arise the medullary rays.

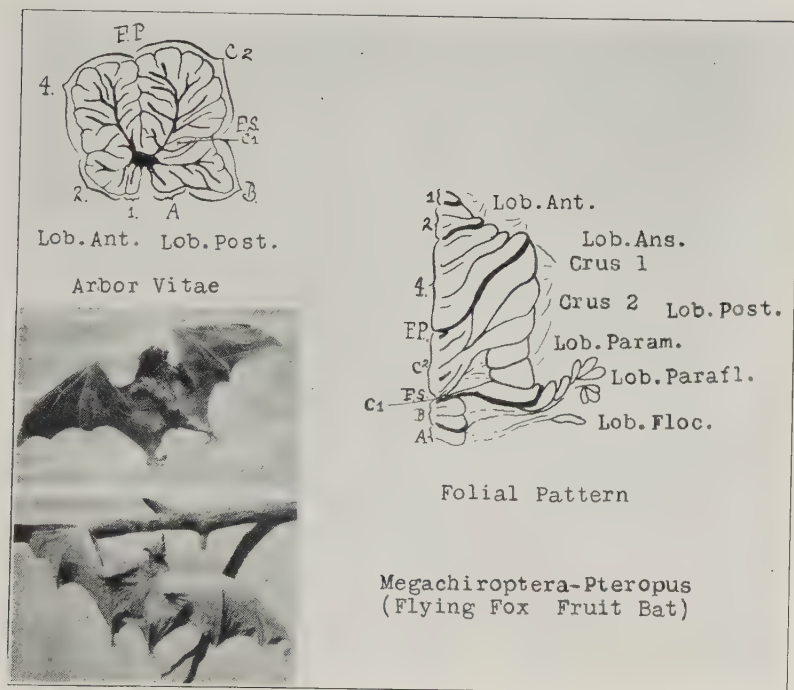


FIG. 29. *Megachiroptera-pteropus* (flying fox or fruit bat)

The medullary rays

In general, the medullary rays are simple and delicate. Ray 1 arises from the ventral aspect of the anterior medullary substance as a single branch. It does not have any reduplications. Ray 2 proceeds directly forward, subdividing into two simple branches. Lobulus 4 presents a small cephalic folium at its base, and then gives off larger cephalic and smaller caudal branches. Ray C arises as a slender extension upward and backward from the medullary substance, proceeding in a curved manner backward and upward and then somewhat forward. It presents

at its lower caudal extremity a single submerged branch which corresponds with ray C 1, being continuous in the folial pattern with the caudal folium of the paramedian formation. The rest of ray C 2 undergoes rather simple division.

Ray B arises as a continuation of the posterior medullary substance. It is a simple stalk, giving off a few branches. Ray A arises as a simple twig from the ventral aspect of the posterior medullary substance.

The lobules

The lobules are relatively simple in arrangement. Lobulus 1 is a single undifferentiated folium. Lobulus 2 is considerably more extensive and presents three folia. Lobulus 4 presents a series of surface folia, subdivided by shallow sulci, and is relatively extensive as compared with lobulus 2. It presents a number of folia in the depths of the fissura primaria. Lobulus C 2 presents a rounded appearance, forming the major portion of the caudal vermis. It is made up of a simple series of folia which do not show any indication of a twist in the vermis pattern. It presents a folium submerged in the fissura secunda which, from its behavior in the folial pattern, shows itself to be lobulus C 1. Lobulus B presents the usual arrangement, except for the caudal prolongation of the apical folium. Lobulus A is a simple, undifferentiated folium.

The folial pattern of Pteropus

The folial pattern of the bat is simple and presents an equal division into anterior and posterior lobes through the presence of the fissura primaria which appears at about the midpoint of the folial pattern, proceeding outward and forward and then outward again in a rather sinuous form. The anterior lobe is considerably less in extent than the posterior lobe. The fissura secunda appears in the usual position between lobuli B and C and continues outward as the caudal limit of the paramedian formation. It bounds the folium which arises in the depth of the fissura secunda as lobulus C 1 and joins the lobulus paramedianus.

Lobulus 1 presents a single undifferentiated vermal folium. Lobulus 2 presents two simple folia which show slight lateral extensions. Lobulus 4 presents three simple folia with medial subdivisions which diminish in size as they approach the periphery. Lobulus C 2 consists of two groups of folia which show vermal characteristics. There is a paramedian sulcus which divides the first three folia from a single folium which extends outward into the hemisphere and may be the representative of the lobulus simplex. Caudal half of lobulus C is apparently connected with the ansiform formation, which is poorly developed, giving only an inkling of the formation of crus 1 and crus 2. There then succeed two rather well defined folia which form the major portion of the lobulus paramedianus. The third folium is relatively wide, and is continuous in the depths of the fissura secunda with the submerged folium which is the only representation of lobulus C 1. The free folia of the lobulus paramedianus are connected by means of a peduncle with the folia of the caudal half of lobulus C 2. Lobulus B presents two single vermal folia. It forms a simple rosette which is continuous outward by means of its peduncle with the base of the lobulus parafloccularis. The lobulus parafloccularis is a simple arrangement of a few folia, terminating in a roset, and then followed again by a

subsidiary small rosette. Lobulus A consists of a single folium which is continuous outward by means of a peduncle with a single folium which represents what there is of the lobulus floccularis.

Lobulus 1 and lobulus 2 share a common peduncular insertion. Lobulus 4 presents an independent peduncle. Lobulus C presents a single broad insertion with the parafoccular implantation, lateral and ventral to it.

Physical characteristics of Pteropus

The bats represent the only order of mammals in which the fore limbs are modified for the purposes of flight, and they alone are able to sustain themselves in the air through true flight. The phalanges, except those of the thumb, are excessively lengthened to support the wing membrane. The extent of this membrane provides an instrument for propulsion and support much more efficient than the wings of the birds and enables the bat to perform aerial acrobatics of a more complicated order than those of the majority of birds. The phalanges of the thumb are short and serve for the purpose of scratching and hanging. The *Chiroptera* have an inordinately keen sense of touch and pressure which seems to be present in the nose-leaves, ears and wing membrane that apparently prevents collisions. This is of special value, since the bats are nocturnal in their activities and possess deficient eyesight. The bats habitually hang by their hind feet, although they can hang by their thumbs. They cannot walk or stand upright, and when on the ground they can only drag themselves along by their thumbs and toe-nails.

The fruit-bat, more properly termed the "flying fox" on account of the shape of its head, is much larger than the other bats, its wing spread often measuring 5 feet. There is no tail or only an extremely rudimentary one, situated ventral to, and usually independent of, the membrane between the hind legs. The fruit-bats are relatively slow and lumbering fliers, the wings moving in long slow sweeps. The head is large, with a blunt muzzle, large flabby and extensive lips and prominent movable ears. The tongue is rather large and freely movable. The eyes are situated anteriorly, with overlapping visual fields, and are conjugated in their movements. The neck is of moderate length and is freely movable. The fore limbs are modified for almost the exclusive function of flying. In hanging, the short thumbs may be used as suspending hooks. The thumbs are also used for scratching. The wings are usually folded, or they may be wrapped about the body. In fighting, the fore limbs are used as clumsy weapons, the thumb claw being of some offensive use. The body is small and without definite characteristics. The hind legs are used chiefly for grasping and hanging; when feeding, the hind legs are used to carry food to the mouth.

HAPALE JACCHUS (MARMOSET)

The arbor vitae of the marmoset presents a rather quadrilateral form, being somewhat more extensive vertically than horizontally. The division of the lobes is rendered evident by the easily identifiable character of the fissura primaria; it is almost vertical and approaches the ventricular fastigium, which is rather narrow and reaches the medullary substance. The fissura primaria and the ventricular

fastigium divide the arbor vitae into practically equal anterior and posterior lobes. The fissura secunda appears in the usual position between lobuli B and C and is almost horizontal, dividing the posterior lobe into a much greater dorsal and a much smaller ventral portion. The medullary substance is simply arranged as an elongated bar without any particular predominance in either the anterior or posterior lobe except for its extension dorsally into the fourth lobule.

The medullary rays

Ray 1 consists of a slender stalk arising from the ventral surface of the anterior medullary substance and bifurcating terminally. Ray 2 arises as a single stout

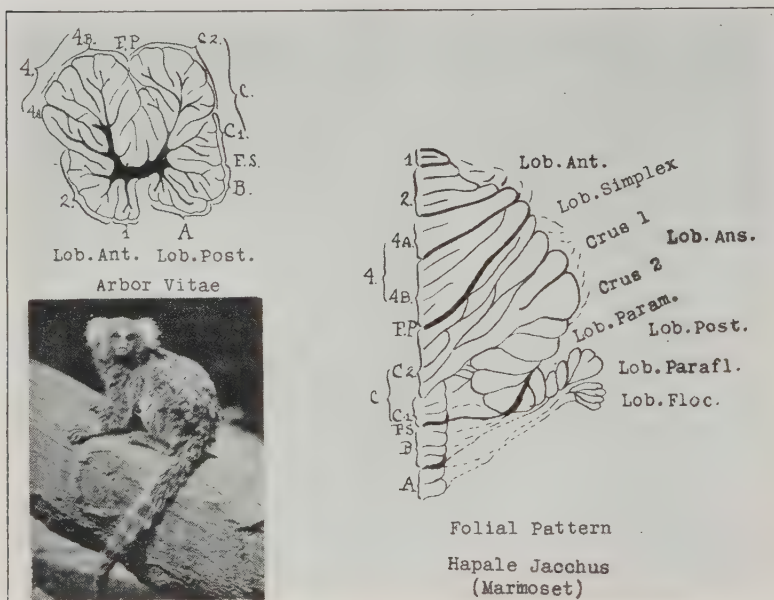


FIG. 30. *Hapale jacchus* (marmoset)

stalk, of larger proportions than the preceding, from the cephalic extremity of the medullary substance. It immediately divides into two subdivisions which do not present any branches but a terminal division. Ray 4 arises as a fairly heavy vertical stalk from the cephalic extremity of the medullary substance. It gives off one long branch forming lobulus 4 A which has only one small dorsal branch. The rest of the stalk then proceeds vertically and subdivides into caudal and dorsal branches. Ray C continues backward and upward from the medullary substance of the posterior lobe, giving off a vertical branch in the depths of the fissura primaria. Ray C then gives off a caudal branch to form ray C 1 and a cephalic branch which

is confined to the fissura primaria. Ray C 2 continues upward as a delicate stem which terminates by dividing into three terminal bifurcated branches. Ray C 1 passes backward and upward, dividing into two terminal divisions. Ray B sweeps backward and slightly downward from the posterior medullary substance, gives off one ventral branch and subdivides. Ray A arises as a single stalk which immediately gives rise to two branches, the cephalic of which at once subdivides, the caudal being continued backward as a long, slender, undivided strip.

The lobules

Lobulus 1 consists of a single undivided folium, and forms the cephalic wall of the ventricular fastigium. Lobulus 2 consists of four wide surface folia arranged in two groups and presents a marked indentation for the reception of the collicular plate. Lobulus 4 is subdivided into a cephalic folium, lobulus 4 A, consisting of a single lamella, and a vertical portion forming lobulus 4 B which, consists of two groups of surface folia and a number of folia in the depths of the fissura primaria. Lobulus C subdivides into two portions, an apical portion representing lobulus C 2, consisting of a number of broad surface folia and forming the summit of the lobulus, and lobulus C 1 which consists of three separate folia. Lobulus B is composed of three unequal surface folia. Lobulus A is simple, forming the caudal boundary of the ventricular fastigium and consisting of a few surface folia.

The folial pattern of Hapale jacchus

The fissura primaria appears at about the middle of the median section and proceeds forward and outward toward the periphery, in a fairly straight course. The fissura secunda divides the posterior lobe into two portions, limiting lobuli B and C and determining the transition between the lobulus paramedianus and the lobulus parafloccularis. Lobulus 1 is a simple folium which is subdivided in the vermal region, but forms a single folium at its termination. Lobulus 2 consists of three folia which extend outward, each one progressively to a greater distance. Lobulus 4 consists of two groups: (1) lobulus 4 A, which, by its disposition, shows its resemblance to lobulus 3 of the pattern of carnivorous animals, and (2) lobulus 4 B, representing the definitive lobulus 4. Lobulus 4 A is subdivided in the vermal region but is reduced to a single folium in its lateral portion. Lobulus 4 B presents vermal divisions but survives as a single lamella at the periphery. Lobulus C is divided into two portions, a cephalic division, C 2, which presents a definite continuity between the vermal and the lateral folia, and lobulus C 1 in which this connection is interrupted. There is a definite indication of a paramedian groove. The cephalic folia of lobulus C 2 are rather irregularly arranged in the territory of the lobulus simplex. These folia are continuous caudally with an ill defined ansiform formaton, there being a simple divided folium of rather large extent representing the major portion of crus 1 and crus 2. The caudal portion of lobulus C, constituting lobulus C 1, consists of vermal folia which are continued outward in the depths of the paramedian sulcus by means of a few submerged folia to the lateral chain. The rest of lobulus C 1 is continuous, by means of a peduncle, with the paramedian formation. The folia succeeding crus 1 appear as two rather broad lamellae, followed by three rather large broad folia representing the lobulus

paramedianus. Lobulus B appears as two chief folia, which have partial subdivisions, forming a rosette the peduncle of which is continuous with the end of the parafloccular formation. The lobulus parafloccularis appears as a direct continuation of the lamellar chain from the lobulus paramedianus, the folia turning forward and continuing to the apex of the lobulus ansiformis, where it terminates in an ill defined, rudimentary rosette. Lobulus A consists of two undivided folia which are continued outward by a peduncle in the direction of the lobulus floccularis. The lobulus floccularis consists of a poorly defined rosette, without any terminal group of folia. It occupies the regular position between the peduncle of the cerebellum and the parafloccular formation.

The anterior lobe presents a single peduncle which serves as an implantation for all of the folia into the medullary substance. The lateral termination of the folia of the posterior lobe present a single implantation which is situated dorsal and mesial to the origin of the folia of the lobulus parafloccularis from the medullary substance.

Physical characteristics of Hapale jacchus

The marmoset is a small animal from 8 to 10 inches in length. It is arboreal and quite adapted to this habitat. The head is small with the eyes situated in the anterior position and thus possessing overlapping fields of vision. The eye movements are well conjugated. The neck is short, but extremely mobile. The limbs are all well differentiated, possessing considerable independence, the fore limbs being more independent than the hind limbs. The fore limbs are, to a considerable extent, freed from the necessities of locomotion, the animal being able to sit up and use its fore limbs as hands. The hind limbs also, to a certain extent function as hands. The body is small. The marmoset is agile and quick in its movements.

LEMUR VARIUS (BLACK AND WHITE LEMUR)

The outline of the arbor vitae of the lemur is practically circular. The fissura primaria appears to be almost directly vertical, ending at the medullary substance directly opposite the ventricular fastigium, which is relatively wide open. These two structures, therefore, divide the arbor vitae into almost equivalent anterior and posterior lobes. The fissura secunda appears below the middle line of the posterior lobe, directed caudally and separating lobuli B and C.

The medullary substance is condensed below the middle of the arbor vitae into two portions marked by a faint constriction as the medullary substance of the anterior and posterior lobes. The anterior medullary substance is continued upward as a strong projection forming the base of ray 4.

The medullary rays

Ray 1 arises as a simple undivided stalk from the ventral aspect of the anterior medullary substance. Ray 2 arises as a rather stout branch from the projection forward of the medullary substance of the anterior lobe and almost immediately divides into two independent stems, the dorsal being more branched than the ventral twig. Ray 3 arises as a fairly heavy, apparently independent shoot from

the dorsal aspect of the anterior medullary substance. It projects forward in a somewhat curved fashion, giving off simple side branches, and ends in a bifurcation. Ray 4 arises as a thick, heavy stalk from the upper portion of the medullary substance. It gives rise to two secondary stems which undergo a moderately intensive secondary division.

The medullary substance of lobulus C consists of three separate groups of rays, the first arising as a simple, vertical stalk, forming a part of the caudal boundary of the fissura primaria; the second arising as a curved thick stem which extends upward as ray C 2, undergoing a fairly complicated terminal division, and the third passing almost directly caudal, as a simple stem undergoing further division.

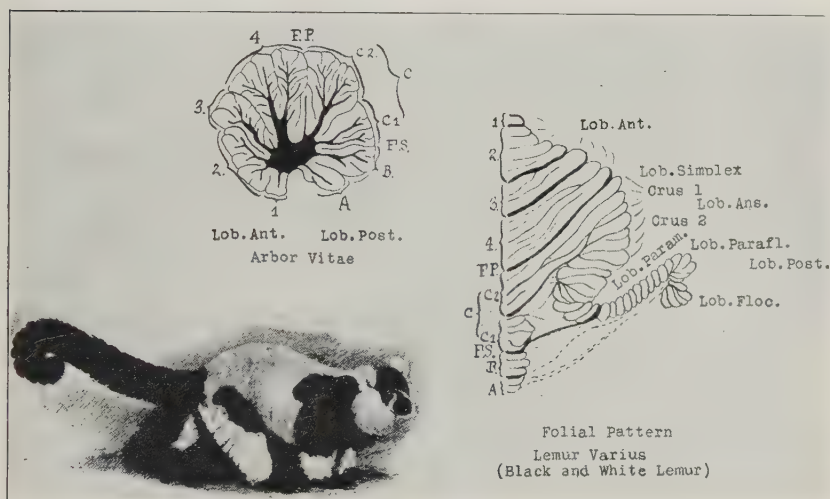


FIG. 31. *Lemur varius* (black and white lemur)

Ray B appears as a single stalk, a direct continuation caudally of the posterior medullary substance. It gives off one side branch ventrally and divides terminally. Ray A is a simple stalk without subdivision.

The lobules

The first lobulus appears as a simple, undivided folium, forming the cephalic boundary of the ventricular fastigium. The second lobulus presents a series of five small folia subdivided into two groups. Lobulus 3 consists of two surface folia and is a narrow elongated lobulus. Lobulus 4 consists of two groups of three folia each. It is the largest lobulus in the arbor vitae. Lobulus C is subdivided into two surface portions, the major division being formed by lobulus C 2 and consisting of two groups of small folia, a rather large folium appearing in the depths of the fissura primaria. Lobulus C 1 consists of two simple divided folia. Lobulus

B is a small lobulus with three definite folia. Lobulus A presents only two successive folia and forms a sloping caudal wall to the ventricular fastigium.

The folial pattern of the black and white lemur

The fissura primaria divides the folial pattern into almost equivalent anterior and posterior lobes, and proceeds outward and forward without any material deviation. The fissura secunda appears between lobuli B and C and is continued outward to demarcate the termination of the lobulus paramedianus and the beginning of the lobulus parafoccularis. Lobulus 1 consists of a single vermal folium. Lobulus 2 consists of two separate portions, the cephalic being largely vermal while the caudal shows both vermal and lateral divisions. Lobulus 3 consists of three median folia which are reduced to one rather large folium at the periphery. Lobulus 4 is divided into two groups of folia, three or four in each subdivision, which become reduced by the termination of the sulci to two rather well defined folia. Lobulus C is divided into two portions, the cephalic of which represents lobulus C 2. Lobulus C 2, in turn, is subdivided into cephalic and caudal portions. The cephalic subdivision consists of two pairs of folia continuous with the lamellae which extend throughout the hemisphere, therefore forming a fairly well defined lobulus simplex. The caudal portion represents the ansiform formation and consists of a lateral group of folia made up of a series of lamellae following directly on the lobulus simplex. The indefinite lobulus ansiformis presents a poorly defined crus 1 and crus 2 which are continuous mesially with the last folium of lobulus C 2 which scarcely shows in the pattern. Crus 2 is continuous with a series of lamellae forming the lobulus paramedianus which is interrupted by a rosette. The caudal group representing lobulus C 1 consists of a vermal group of folia forming a rosette, the peduncle of which is continued outward to be continuous with three or four surface folia, the lobulus paramedianus, which turns outward caudally and is separated from the beginning of the lobulus parafoccularis by the lateral continuation of the fissura secunda. Lobulus B consists of three simple folia arranged in a rosette the peduncle of which is continuous outward with the base of the parafoccular formation. The parafocculus consists of a simple series of folia skirting the edge of the lobulus paramedianus and the lobulus ansiformis, reaching the lobulus simplex and turning on itself in the form of a rosette to terminate without the development of an uncus terminalis. Lobulus A consists of two small vermal folia based on a peduncle which is continued outward in the direction of the lobulus floccularis. The lobulus floccularis consists of a simple folial rosette, situated between the cerebellar peduncle and the parafoccular formation.

The lobules are implanted into the medullary substance in a rather indefinite manner. All of the folia of the anterior lobe seem to converge together in a single implantation, while a similar single implantation serves for the lobulus simplex, the lobulus ansiformis and the paramedian formation. The lobulus parafoccularis is based directly on the medullary substance, lateral and ventral to the attachment of the rest of the posterior lobe.

Physical characteristics of Lemur varius

Lemur varius is nocturnal and chiefly arboreal in its habits. It is relatively small, not over 2 feet (60.9 cm.) in length. It is an excellent climber. The head is small, and the eyes are situated well forward and have overlapping fields of vision and well conjugated movements. The ears are rounded and freely movable. The neck is rather short and mobile. The tongue is long and can be extended from the mouth. The body is of moderate size. The limbs are of unequal length, the hind legs being somewhat longer. The fore limbs terminate in well formed hands with functioning thumbs which are apposable. The hind limbs also possess well formed and manually functioning extremities. There is a considerable degree of unilateral independence in both the fore and the hind limbs, that of the former being greater. The tail is of considerable length and is prehensile. The hands are well differentiated and the lemur is capable of sitting up and using its hands as explorers of the environment and to obtain and insert food into the mouth. It can also pick up objects and examine them with the hands and fingers. *Lemur varius* is a rather active animal; it possesses a considerable degree of agility and can leap from bough to bough with speed and accuracy.

MACACUS RHESUS (MACAQUE)

The arbor vitae of the macaque presents a more or less rounded or oval form, the cephalocaudal diameter being somewhat greater than the vertical. The fissura primaria appears as a well defined, almost vertical sulcus, with a slight inclination downward and forward. It approaches the ventricular fastigium, producing a constriction in the medullary substance between the fissura and the fastigium. The fissura primaria and the ventricular fastigium divide the arbor vitae into about equal anterior and posterior lobes. The fissura secunda appears in the usual position between lobuli B and C and divides the posterior lobe into a smaller ventral and a larger dorsal portion. The medullary substance presents a marked constriction dividing it distinctly into the medullary substance of the anterior and posterior lobes, appearing as two rather large condensations, the mass in the anterior being considerably larger than that in the posterior lobe. The entire arbor vitae is considerably larger than that of the two preceding primates, and the lobulation is much more extensive owing to the greater arborization of the medullary substance.

The medullary rays

Ray 1 appears as a simple undivided twig arising from the ventral surface of the anterior medullary substance and proceeding directly downward. Ray 2 arises as a pair of independent branches from the extension forward of the medullary substance, the first being a small stem which gives off lateral divisions, and the second a much larger stalk which proceeds directly forward giving rise to a ventral and a larger dorsal branch. Ray 4 consists of a heavy prolongation upward of the medullary substance which immediately divides into a cephalic branch that gives off side branches, and a vertical branch that continues directly upward and divides into two stalks. It presents a number of rather fine branches in the depths of the fissura primaria. Ray C arises as a direct prolongation upward and backward of the posterior medullary substance. It is rather heavy stalk which divides

into a substantial cephalic more or less perpendicular branch, giving off cephalic and caudal branches. Ray C 1 proceeds more horizontally and divides into lateral and terminal branches. Ray B arises as a stem directed backward from the mass of the medullary substance, giving off rather extensive side branches and bifurcations. Ray A springs as a thin stalk from the ventral surface of the posterior medullary substance and continues downward and backward, giving off side branches.

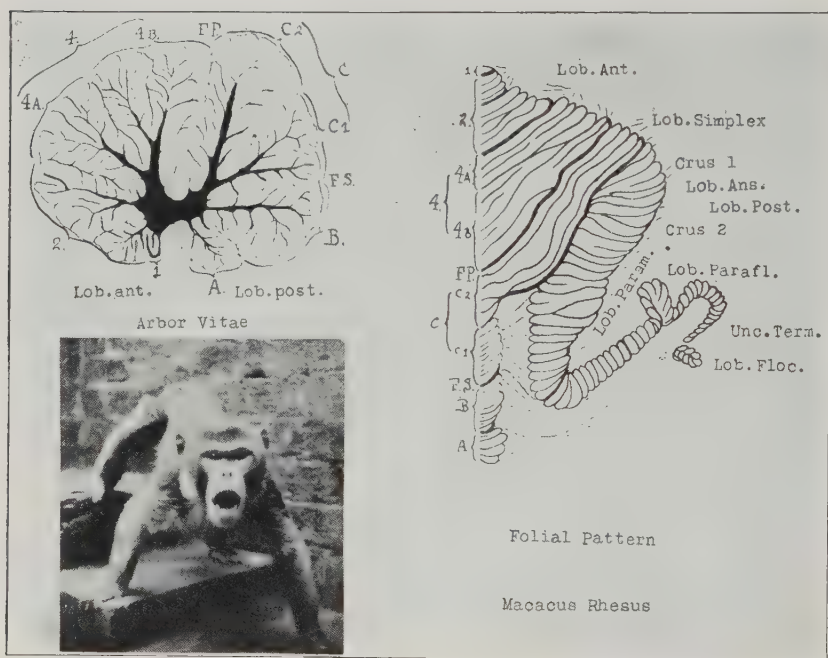


FIG. 32. *Macacus rhesus* (macaque)

The lobules

Lobulus 1 is a simple folium forming the cephalic margin of the ventricular fastigium. Lobulus 2 is a much more extensive lobulus subdivided into three distinct portions. Lobulus 4 is divided into two separate portions of about equal size, both of which are further differentiated into two folial groups. It presents a considerable number of folia in the cephalic wall of the fissura primaria. Lobulus C is subdivided into two portions. Lobulus C 2 is rather small, and consists of a number of broad surface folia. Lobulus C 1 is subdivided into two smaller derivatives. Lobulus B is a rather extensive lobulus. Its terminal portion consists of a group of folia derived from the main continuation of the medullary ray and a

rather extensive ventral group of folia. Lobulus A consists of a simple lobulus forming the caudal boundary of the fastigium.

The folial pattern of Macacus rhesus

The fissura primaria divides the folial pattern into a distinctly larger anterior lobe and a comparatively simple posterior lobe. It proceeds almost directly outward and forward, without any material curves or sinuosities. The fissura secunda appears in the usual position, separating lobuli B and C, and continues outward to limit caudally the lobulus paramedianus. Lobulus 1 consists of a single vermal folium. Lobulus 2 consists of two separate portions, the cephalic being distinctly vermal in character, while the caudal division presents a definite prolongation outward into the lateral substance, each successive folium being longer than the preceding lamella. Lobulus 4 is divided into two definite groups. The cephalic division, lobulus 4 A, presents a simple arrangement of three folia, all of which reach the periphery. Lobulus 4 B shows a definite division into vermal and lateral portions, with some irregularity in the arrangement of the folia, there being a considerable reduction in number and extent of the folia, from six in the region of the vermis to two in the periphery. Lobulus C again presents a distinct differentiation into cephalic and caudal portions, lobuli C 2 and C 1. In the former, the vermal folia are directly continuous with the simply arranged striplike folia of the lobulus simplex. There are a few caudal terminal vermal folia. Lobulus C 1 consists of vermal folia which converge on a rather broad peduncle which spreads out to become continuous with most of the ansiform formation and the lobulus paramedianus. The lobulus ansiformis presents a poorly defined crus 1 and crus 2, there being but little differentiation between this formation and the regularly arranged folial chain representing the lobulus paramedianus, which continues backward to its delimitation by the fissura secunda. Lobulus B consists of a group of vermal folia based on a peduncle which extends outward and is continuous with the base of the parafloccular formation. The paraflocculus arises as a gradual turn from the lobulus paramedianus into a long serial arranged group of folia, constituting the lobulus parafloccularis, which continues forward to the region of the apex of the ansiform formation. A distinct rosette is formed at this point, following which the chain continues forward, then turns outward and finally proceeds backward, to form an uncus terminalis. Lobulus A consists of a simple group of vermal folia with a peduncle which merges into the medullary substance. The lobulus floccularis consists of a simple folial rosette and lies between the peduncle of the cerebellum and the floccular formation.

The insertion of the various lobes into the medullary substance takes place as follows: The first and the cephalic part of the second lobuli are inserted together, and the caudal part of the second with the third and fourth lobuli are inserted by means of a single peduncle. Lobulus simplex, lobulus ansiformis and lobulus paramedianus have a broad support on the medullary substance, while lateral and ventral to them is found the medullary insertion of the lobulus parafloccularis.

Physical characteristics of Macacus rhesus

Macacus rhesus is a fairly heavily built monkey of moderate size. The head is large and massive; the eyes, situated anteriorly, possess overlapping fields of vision and are well conjugated. The jaws are heavy; the tongue is of good size and is freely movable. The neck is rather short and heavy. The body is rather slight; the upper extremities are heavy and long, and terminate in good, functional hands with rather long fingers and a short thumb which is quite apposable. The macaque can use its hands as such extensively. Its hind limbs are not so heavy and strong as the fore limbs, are shorter and are used chiefly as a means of support, although the feet are considerably more manual than are the hind limbs of *Cynocephalus*. The hind legs are used chiefly for scratching, running, jumping, etc. The macaque is at home on the ground, although he is predominantly arboreal in his activity. The macaque can be readily taught to walk upright. The tail is short and without special function. It is not prehensile.

CYNOCEPHALUS BABUIN (BABOON)

The arbor vitae of the baboon presents an outline which, while circular, is beginning to show the steady evolution of lobulus C 2 which, with the shift in the position of the medullary substance, is the major developmental process in the primate series. The fissura primaria is almost vertical in location and directly approaches the ventricular fastigium which is deep but rather wide. The arbor vitae is divided by these two structures into two almost equivalent halves, the posterior lobe being slightly greater than the anterior lobe. The medullary substance presents a marked constriction in the region of the approach of the fissura primaria to the ventricular fastigium, with a marked enlargement in the anterior lobe and a long drawn-out extension in the posterior lobe.

There is a marked increase in the branching of the medullary tree and a consequent advance in cerebellar foliation.

The medullary rays

Ray 1 appears as a lingula based on the superior medullary velum. Ray 2 develops from the cephalic protrusion of the medullary substance as two independent stalks, the ventral being somewhat simpler and less extensive than the dorsal branch. There is a distinct ray 3 which arises from the dorsal aspect of the medullary substance, proceeds forward in a curved fashion and divides terminally, having given off numerous side branches. Ray 4 arises almost directly perpendicularly from the dorsal aspect of the medullary substance, and gives off side branches and a cephalic division of considerable proportion which proceeds upward, giving off lateral branches. The vertical division gives off a number of stout caudal branches which make up the folia which form the fissura primaria cephalically. Ray C 2 is drawn out caudally and upward, giving off long cephalic branches in the depths of the fissura primaria and short caudal branches. It then undergoes a rather extensive terminal arborization. Ray C 1 is given off as a moderately thick stem close to the origin of ray C which proceeds backward and upward, dividing and giving rise to numerous lateral branches. Ray B arises as a thick heavy stem

close to the origin of ray C, and gives off a series of short dorsal and longer and more richly developed ventral branches. Ray A is a simple stem, close to the ventricular fastigium, which gives rise to a number of lateral branches and a terminal bifurcation.

The lobules

Lobulus 1 appears as a lingula developed on the superior medullary velum and forms the cephalic wall of the ventricular fastigium. Lobulus 2 is composed of three separate folial groups, the second and third being formed by the division of the dorsal medullary ray. The first folial group is formed of two subdivided

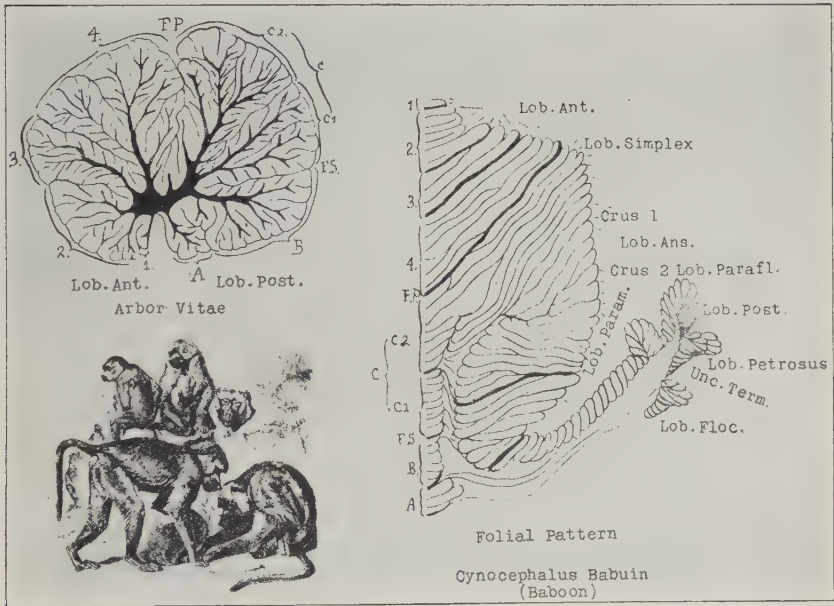


FIG. 33. *Cynocephalus babuin* (baboon)

folia supported by the ventral medullary ray. The second and third groups are composed of two folia each, which are developed on the divided dorsal medullary ray. They are rather wide and relatively simple. Lobulus 3 is long and narrow, presenting a considerable degree of foliation in its contacts with lobulus 2 and lobulus 4, and divided at its summit into two folial groups. Lobulus 4 presents the usual division into a cephalic and a caudal group. The cephalic group is not given the designation of lobulus 4 A on account of the relative lightness of the medullary ray. It is a conical lobulus, its base being formed by two folial groups. the remainder of lobulus 4, the usual lobulus 4 B, constitutes a moderately well developed sublobulus composed of a number of surface folia and a fairly well

developed foliation in the depths of the fissura primaria. Lobulus C definitely indicates the efflorescence in lobulus C 2, which is the distinguishing feature in the progressive development of the primate cerebellum. The medullary branching is extensive, and the foliation is correspondingly increased. The spray of terminal branches is beginning to assume human proportions. Lobulus C 1 is conical, and its base occupies a considerable portion of the surface. Lobulus B is relatively quadrilateral, on account of the development of the second ventral branch, and it presents a considerable number of surface folia. Lobulus A forms the caudal wall of the ventricular fastigium and is a relatively simple lobulus.

The folial pattern of Cynocephalus babuin

The fissura primaria appears somewhat cephalad to the middle of the vermis, and proceeds in an almost straight line forward and outward. It divides the folial surface into a much smaller anterior and a much larger posterior lobe. The fissura secunda appears between lobuli B and C and is continued outward to limit caudally the lobulus paramedianus. The anterior lobe, with its long regular folia, is assuming definite human characteristics, while the posterior lobe is still clearly infrahuman in its organization. Lobulus 1 presents a single vermal folium. Lobulus 2 consists of three vermal folia, two of which are subdivided, and a terminal folium which presents a definite lateral extension. Lobulus 3 consists of three vermal folia, the cephalic one of which loses itself in the fissure between lobuli 2 and 3, while the remaining two continue outward as straight strips to the periphery. Lobulus 4 consists of a group of folia, the majority of which reach the periphery, only a few disappearing in adjacent fissures. Lobulus C presents two portions, a lobulus C 2 and a lobulus C 1. Lobulus C 2 presents a differentiation into cephalic and caudal divisions. The cephalic portion shows a direct continuity between the group of vermal folia and the lateral extensions which run outward parallel to the fissura primaria, representing the lobulus simplex. This portion is succeeded by a group of folia separated by a paramedian fissure into vermal lamellae and simple striplike lateral folia which are indirectly continuous with the vermal subdivisions. A group of folia then follows which represent a fairly definite lobulus ansiformis with a crus 1 and a crus 2. Crus 1 consists of a small number of folia which directly succeed the striplike folia of the more cephalic portion of the lobulus. There is no distinct apex to the ansiform formation. Crus 2 consists of a group of wide folia which gradually returns toward the midline, producing a fairly definite sulcus intercruralis, and is joined by means of a peduncle with the caudal folia of lobulus C 2. Lobulus C 1 presents a group of uniform vermal folia which is continued laterally by means of a peduncle that joins a group of rapidly diminishing folia which directly succeeds crus 2 and forms the lobulus paramedianus. The paramedian lamellar chain turns outward to its termination at the fissura secunda. Lobulus B presents a simple group of vermal folia forming a rosette, the peduncle of which is directly continuous with the base of the lobulus parafoccularis. The lobulus parafoccularis presents a slow transition from the terminal folia of the lobulus paramedianus into the lobulus parafoccularis. The lobulus parafoccularis is continued forward and outward under cover of the lobulus paramedianus and the ansiform formation as a chain of lamellae which, near its cephalic extremity at the

apex of the lobulus ansiformis, presents a triple rosette formation, the terminal rosette being a definite lobulus petrosus ending in a reduced uncus terminalis. Lobulus A consists of three vermal folia forming a roset which is based on a peduncle that fades away into the medullary substance in the direction of the lobulus floccularis. The lobulus floccularis begins in close connection with the uncus terminalis of the lobulus parafloccularis as a folial rosette and then dwindles away in a diminishing series of folia.

The lobules are implanted into the medullary substance by means of a few simple peduncles. The small first lobulus presents a separate implantation. The second, third and fourth lobuli possess a common implantation. The remainder of the hemisphere is implanted in a linear fashion along the beginning of the sulcus horizontalis magnus where the cerebellum is folded on itself.

Physical characteristics of Cynocephalus babuin

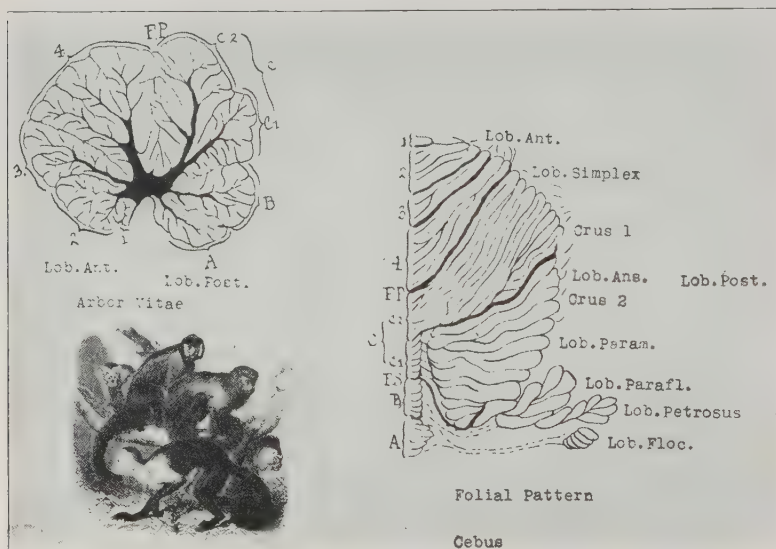
Cynocephalus babuin belongs to the dog-faced baboons. The animal is large, about the size of a large dog, but considerably more powerful and much heavier. Its head is rather massive, with a protruding snout which carries the nostrils. The eyes are situated anteriorly and possess overlapping fields of vision; they are well conjugated in their movements. The jaws are heavy, and the tongue is of moderate size and mobile. The neck is of moderate length and freely movable. The body is long and is supported by the four limbs, the hind limbs being longer than the fore limbs. The tail is short. This animal is terrestrial, frequenting both dry and stony localities. It is quite powerful, the fore limbs being especially well developed. The baboon walks on all fours, the hands being placed flat down on the ground with the head bent downward. The fore limbs are used independently to turn over sticks, stones, etc., in the search for food. Both the fore and hind limbs are unilaterally independent, the former to a much greater extent. It is a rather awkward, ungainly animal and is not possessed of any great speed.

CEBUS

The arbor vitae of the cebus presents a more or less circular form. The fissura primaria is easily identifiable as a vertical sulcus descending toward the ventricular fastigium which is relatively wide open and not deep. These two structures divide the arbor vitae into two lobes, anterior and posterior, which are about equal in extent. The fissura secunda appears between lobuli B and C, directed from before backward and upward. The medullary substance is condensed in the center, presenting approximately equal portions in the anterior and posterior lobes separated by a slight constriction. The medullary substance of the anterior lobe appears heavier on account of the heavy ray 4. The arbor vitae is not so richly developed as is that of *Cynocephalus*, but the organization of lobulus C 2 seems to indicate a further advance in the primate series over that presented by *Cynocephalus*, and more in the line with the human type. The lighter architecture of the cerebellum may be due to the much smaller corporeal bulk of the cebus as compared with that of the baboon. The cebus is definitely more bimanual than the baboon.

The medullary rays

Ray 1 appears as a lingula, based on the superior medullary velum. Ray 2 arises as a direct extension forward of the anterior medullary substance, giving rise at once to two subdivisions which again subdivide, the dorsal more richly than the ventral branch. Ray 3 arises as an independent stem from the dorsal and cephalic aspect of the medullary substance. It forms a long, slender ray, gives off lateral branches and bifurcates. Ray 4 arises as a marked extension upward of the anterior medullary substance, giving rise to a cephalic branch which, if heavier, would be called ray 4 A, and then continuing upward as a ventral branch again subdivides, giving rise to lateral and terminal subdivisions as ray 4. There are

FIG. 34. *Cebus*

a few simple branches from the caudal aspect of ray 4. Ray C arises as a direct extension upward and backward from the posterior medullary substance as a rather stout stem which divides at once into two subsidiary branches, a cephalic ray C 2 which continues upward in a curved fashion forward, giving off one cephalic branch and then smaller caudal and terminal branches. Ray C 1 proceeds more obliquely, backward and upward, giving off a greater number of ventral branches, and subdivides into a terminal group. Ray B arises as a direct extension backward of the medullary substance, giving off lateral branches and subdividing. Ray A arises as a single stem from the ventral aspect of the medullary substance, and curves downward and backward, giving off lateral branches.

The lobules

Lobulus 1 consists of three or four folia based on the superior medullary velum as a lingua. Lobulus 2 consists of two subgroups of folia, the ventral subdivision being a single group of folia, while the dorsal subdivision presents two folial groups. The surface folia are rather wide. Lobulus 3 is a long, narrow conical lobulus which presents a number of submerged folia and a basal group of two folial clusters. Lobulus 4 is a rather large conical lobulus which is subdivided into two main sublobules. The cephalic division is rather narrow and presents two surface folia. The caudal division is much wider, makes up the greater part of the lobulus and is divided into two surface groups of folia, there being a number of simple submerged folia in the fissura primaria. Lobulus C is relatively simple in the arbor vitae, but much more extensive in the folial pattern. It is relatively delicate in its architecture, and presents a rather large folial group in the fissura primaria and a series of surface folia. Lobulus C 1 is triangular, its ventral portion being made up of a number of folia, while its free surface is made up of two definite folial groups. Lobulus B is well developed and presents two groups of surface folia. Lobulus A is rather long drawn-out and forms a rather sloping caudal wall for the ventricular fastigium.

The folial pattern of Cebus

The folial pattern presents a beginning expansion in the region of the lobulus ansiformis which will be found to be the predominating change in the primate series. This rather extensive development is rather surprising in view of the simple organization of lobulus C in the arbor vitae. The fissura primaria divides the pattern into a small anterior lobe and a larger posterior lobe, arising at about the middle of the folial pattern and proceeding forward and outward. The fissura secunda appears between lobuli B and C and serves to differentiate the termination of the lobulus paramedianus from the lobulus parafloccularis. The development of the anterior lobe and the lobulus ansiformis presents a definite advance over that shown in the baboon toward the human type.

Lobulus 1 consists of a single undifferentiated surface vermal folium as the lingua. Lobulus 2 shows a distinct differentiation into the vermal and lateral portions by the direction and inclination of the sulci, which produce five folia at the median line, which are reduced to two at the periphery of the lobulus. Lobulus 3 is a narrow lobulus beginning as three folia which are reduced to two and then to one. Lobulus 4 shows a distinct differentiation into a vermal and lateral region, the sulci tending to approach each other and run into the preceding fissures, seven folia being reduced to two in the lateral extremity of the lobe. Lobulus C is subdivided into a cephalic lobulus C 2 and a caudal lobulus C 1. The vermal folia of lobulus C 2 are directly continuous with long striplike lateral folia which run upward forming a well defined lobulus simplex. Many of these sulci fail to reach the periphery. Following the folia of the fairly well defined lobulus simplex, there ensues a gradually diminishing series of folia which forms a rather undifferentiated crus 1, which turns on itself, and, with a rather long folium, forms an indefinite crus 2. A large number of the caudal folia arise from the fissure separating lobuli C 2 and C 1. Lobulus C 1 presents a definite separation between the

vermal and the lateral folia. The vermal folia consist of six small surface folia drawn together into a peduncle which spreads out to become continuous in the depths with the folia forming crus 2 and an irregular series of wide folia, the lobulus paramedianus. These folia rapidly are reduced in width and terminate in a curved series of folia which is limited by the lateral extension of the fissura secunda. Lobulus B consists of a vermal series forming a rosette, the peduncle of which continues outward around the base of the lobulus paramedianus into the beginning of the lobulus parafoccularis. The lobulus parafoccularis consists of a loosely arranged group of folia representing a poorly defined rosette which is applied along the lateral surface and undersurface of the lobulus paramedianus. It is continued still further forward and then outward into a well defined rosette which forms a lobulus petrosus. Lobulus A consists of a group of vermal folia in the form of a rosette, the peduncle of which merges into the medullary substance in the general direction of the lobulus floccularis. The lobulus floccularis consists of a simple series of folia, without any distinct rosette formation.

The entire anterior lobe presents one medullary implantation, while the cephalic portion of the posterior lobe has a similar broad base, with the paramedian and parafoccular formations ventral and lateral to it.

Physical characteristics of Cebus

Cebus represents the well known specimen of monkey customarily seen with organ grinders. It is of moderate size, with fairly long extremities and a relatively small body. The head is of fair size, the ears are small and the eyes are placed well forward in the anterior position. The eyes possess overlapping fields of vision and are well conjugated in their movements. The neck is of moderate length and is freely movable. The limbs are rather long and slender. All four extremities are used in progression. This monkey places the palms of the hands on the ground in walking, unlike the old world monkeys. Both the hands and the feet possess manual characteristics and are bilaterally independent, the fore limbs being more independent of one another than the hind limbs. The thumbs are not appposable rising at a considerable distance above the fingers and being short and used as fingers. The tail is usually long, is actively prehensile and acts as a fifth extremity in climbing, maintaining position and other functions. This monkey is agile and quick in its movements. The fore limbs are extremely well coordinated, since cebus is able to catch flies and other insects with its hands. It is arboreal in its habitat, being perfectly at home in the trees, swinging, climbing and running along the limbs and jumping from one branch to another.

ATELES ATER (SPIDER MONKEY)

The arbor vitae of the spider monkey presents a more or less rounded outline. The fissura primaria appears somewhat in front of the middle of the arbor vitae and is directed from above downward and forward toward the ventricular fastigium which is rather deep and moderately wide. The arbor vitae is, therefore, subdivided into a smaller anterior and a larger posterior lobe. The fissura secunda occupies its usual position between lobuli B and C and is directed horizontally.

The medullary substance appears as a heavy mass in the center of the cerebellum, with a slight constriction between the fissura primaria and the ventricular fastigium. It presents an enlargement as it passes into the anterior lobe, but is rather reduced in the posterior lobe. The arborization is considerably increased over that found in *Cebus*, and the foliation is correspondingly more complicated. The medullary rays of the posterior lobe are rather heavy.

The medullary rays

Ray 1 appears as a long slender filament from the ventral aspect of the anterior medullary substance. It presents a terminal bifurcation. Ray 2 arises as two

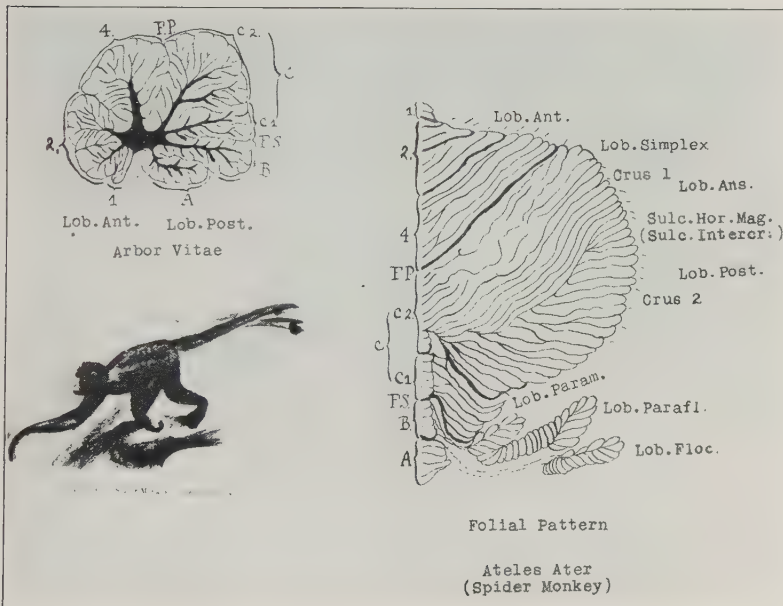


FIG. 35. *Ateles ater* (spider monkey)

definite independent branches from the protrusion forward of the anterior medullary substance. The first is directed downward and forward, and the second upward and forward, each one subdividing—the dorsal stem somewhat more extensively—into lateral and terminal branches. Ray 4 is a heavy projection upward of the medullary substance which gives rise to a number of slender lateral branches both cephalically and caudally, while at its summit a number of fine twigs arise. Ray C 2 and Ray C 1 arise by means of a common trunk from the dorsocaudal angle of the medullary substance; the ascending branch ray C 2 passes backward and upward, giving rise to cephalic branches and a stout caudal branch which plays

an important rôle in the expansion of lobulus C 2 in the hemisphere. The horizontal branch continues backward, giving off lateral branches as ray C 1, and subdivides. Ray B arises from the ventrocaudal angle of the medullary substance as a relatively long heavy stem, giving off lateral branches and subdividing terminally. Ray A arises from the ventral aspect of the medullary substance, proceeds downward and then curves backward, giving off lateral branches.

The lobules

Lobulus 1 appears as a long, narrow folium, presenting on its free surface a subdivision into two folia. It forms the cephalic margin of the ventricular fastigium. Lobulus 2 is extensive, and is composed of two subdivisions. The first comprises a rather conical group of folia which appear on the surface as two rather wide folia. The second or dorsal division appears as two definite folial groups which result from the division of the medullary ray. The lobulus is triangular in shape, and presents a number of folia in the fissures between lobulus 2 and lobuli 1 and 4. Lobulus 4 is still larger, triangular in shape and made up of a considerable series of narrow folia in the depths of the fissures limiting the lobulus. Its surface expression is composed of two rather poorly defined folial groups. Lobulus C comprises about two thirds of the posterior lobe and is divided into a prominent lobulus C 2 and an inconspicuous lobulus C 1. Lobulus C 2 is triangular and presents on the surface a fairly simple group of folia. It presents, however, a prominent subdivision in its caudal portion which has a relatively heavy medullary stalk and apparently expands in the fissure between lobulus C 2 and lobulus C 1 into a considerable overgrowth which represents the major caudal portion of the lobulus ansiformis anticipating the human type, in which a small arbor folial group gives rise to an extensive hemispherical expansion. Lobulus C 1 is narrow, with a number of lateral folia presenting two folial subgroups. Lobulus B is similar and long and narrow, with two groups of surface folia. Lobulus A is a curved group of lamellae which form the caudal wall of the ventricular fastigium; it is continued caudally under the cover of lobulus B.

The folial pattern of Ateles ater

The folial pattern of the spider monkey exhibits a marked increase in the extent and organization of the lobulus ansiformis. The division into anterior and posterior lobes is produced by the fissura primaria which begins at a point somewhat cephalad to the middle of the vermis and proceeds almost directly outward. The fissura secunda appears in the usual position between lobuli B and C, and indicates the termination of the lobulus paramedianus. Lobulus 1 consists of two vermal folia. Lobulus 2 is constituted by two folial groups, cephalic and caudal, the latter being rather more extensive than the former. Each succeeding folium exceeds the preceding, the caudal group being disposed in a more oblique direction. Lobulus 4 consists of a simple group of folia, the vermal portions of which show a distinct tendency to form a paramedian sulcus. The lateral extensions are striplike folia which proceed directly outward with an orderly disposition. Lobulus C presents a division, primarily into two portions, lobulus C 2 and lobulus C 1. Lobulus C 2

presents a further differentiation into dissimilar cephalic and caudal portions. The cephalic division presents distinct connections between the vermal and lateral portions of the folia, while the caudal section presents a distinct paramedian separation between the vermal and lateral portions of the folia. The distinction between the two parts of the folia is shown by the change in the direction of the sulci and the separation of the parts of the folia. The sulci of the cephalic division, as they proceed outward into the lateral hemisphere, become wavy, irregular and broken, forming a poorly defined lobulus simplex. There then succeeds a group of long, wavy folia which continue outward from a peduncular origin from the arbor vitae to the periphery, indicating the production of a crus 1. This group of folia is then terminated by a series of short folia which form the apex of the lobulus ansiformis, following which there is a chain of folia of intermediate length the median prolongations of which come into contact with the folia of crus 1, thus forming a distinct sulcus intercruralis. These folia continue backward, their mesial extremities showing a tendency to curl under the preceding folia and become continuous by means of a peduncle with the vermal folia of the caudal portion of lobulus C 2, which have already been mentioned in the comment on the arbor vitae. Lobulus C 1 forms a group of vermal folia which is directly continuous laterally with the folia succeeding the folia of crus 2, thus forming an irregular but well defined lobulus paramedianus, limited caudally by the fissura secunda. The lobulus ansiformis and lobulus paramedianus thus present definite anthropoid characteristics. Lobulus B presents a simple group of vermal folia which forms a peduncle continuous with the base of the lobulus parafl occularis. The lobulus, parafl occularis begins at the termination of the lobulus paramedianus as a rosette which is applied to the lateral surface of the lobulus paramedianus, and then continues forward by means of a series of narrow folia to end in a recurved tip forming a definite rosette without an uncus terminalis. Lobulus A presents a simple group of vermal folia which forms a peduncle proceeding outward in the general direction of the lobulus fl occularis. The lobulus fl occularis is a rather extensive folial rosette followed by a group of diminishing folia situated between the peduncle and the lobulus parafl occularis.

The medullary implantation is carried still further toward the human type through the origin of the entire anterior lobe by a broad base from the medullary substance. The lobulus ansiformis and the lobulus paramedianus present a similar broad implantation. These two broad implantations focus a little cephalad of the apex of the ansiform formation, thus laying the basis for the formation of the sulcus horizontalis magnus, which in the human cerebellum marks the approximation of the medullary implantation for the anterior and posterior lobes, and is continued into the hemisphere as the sulcus intercruralis. The lobulus parafl occularis is based on the medullary substance, ventral and lateral to the implantation of the lobuli ansiformis and paramedianus.

Physical characteristics of Ateles ater

The spider monkey is easily recognizable from the length of its limbs, the absence of the thumb and the exceedingly prehensile tail. It presents an adaption to an arboreal environment greater than that of any other monkey with the exception

of the gibbon, as shown by its extreme agility in the use of its limbs and tail in passing, climbing, catching and jumping with great rapidity among the branches of the trees. The tail has been developed to an exquisitely adapted fifth limb; there is even a saying that it can catch fish with its tail. It shows a greater unilateral independence of the fore and hind limbs than any of the apes, being able to carry on independent activities with all five members. As Hutchinson says, "It will hold fruit in one hand, find more with one foot, carry food to the mouth with another hand and walk and swing from branch to branch with the tail and the other foot, all simultaneously." The fore limbs show the greatest flexibility. It is able to walk erect, and, when it is doing so, the tail aids greatly in equilibration and is often extended forward over the head as an investigator of the environment. The head is rather small; the eyes are situated anteriorly, with overlapping fields of vision, and are conjugated in their movements. The neck is short and freely movable. The body is rather thin and slight.

SIMIA SATYRUS (ORANG-UTAN)

The arbor vitae of the orang presents a distinct step forward toward the human type in three definite characteristics; the medullary substance is distinctly concentrated in the center; ray 4 is assuming an appearance similar to that of the human stalk, and the tendency already begun in *Ateles*, of the mushrooming upward and backward of lobulus C 2, is definitely advanced in *Simia*.

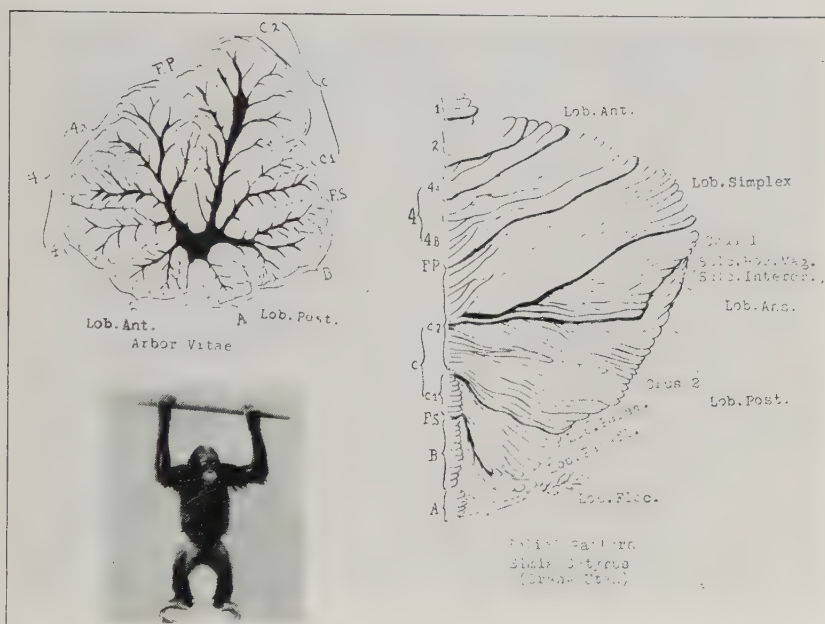
The arbor vitae presents a definitely conical form, the apex of the cone being formed by lobulus C 2. The fissura primaria is situated almost directly in the midline, being nearly perpendicular. Its ventral termination is situated almost directly opposite the fastigial recess which approaches, but does not quite reach, the medullary substance. The arbor vitae shows a distinct separation into an anterior and a posterior lobe, the latter being considerably larger on account of the extensive development of lobulus C 2. The fissura secunda is situated in its usual position between lobuli B and C, and is directed somewhat from before upward and backward.

The medullary substance is concentrated in the center of the cerebellum in a somewhat narrow V-shaped fashion, the limbs of the V being formed by the strong processes 4 B and C 2. The mass of the medullary substance is rather condensed and shows a constriction between the portion which lies in the anterior lobe and that lying in the posterior lobe. The character of the arborization of the medullary tree and the consequent foliation shows a considerable degree of differentiation and strongly resembles the human type.

The medullary rays

Ray 1 appears as a definite lingula, a few folia being disposed on the superior medullary velum. There is no distinct medullary ray. Ray 2 arises from the cephalic extremity of the anterior medullary substance, as a moderately strong process, extending forward and downward, and dividing at once into two definite stalks which give off lateral branches and end in a terminal bifurcation. Lobulus 4 arises as a strong, stout upward extension from the dorsal aspect of the anterior

medullary substance, directed upward and slightly forward, and giving off a strong process cephalically close to its origin, which subdivides the lobulus into lobuli 4 A and 4 B. This cephalic stalk extends forward, giving off lateral branches, and ends in a terminal division. The main stem proceeds upward dividing into a strong cephalic branch which gives off numerous lateral twigs, a decided terminal bifurcation and a smaller caudal process in the fissura primaria. The caudal division of the terminal bifurcation forms the summits of lobulus 4 B. Both of these branches are extensively subdivided. Ray C 2 arises as a strong process directed somewhat obliquely upward and backward from the dorsal aspect of the posterior medullary substance. It is a heavy stalk, giving off strong cephalic branches which

FIG. 36. *Simia satyrus* (Orang-utan)

lie in the depths of the fissura primaria, and a series of caudal stems which expand tremendously in the hemisphere. The ray proceeds upward and gives rise to a spray of branches which forms the summit of the lobulus and is connected with an extensive expansion in the hemisphere. Lobulus C 1 possesses an almost independent origin from the posterior medullary substance, being situated about midway between the origin of rays B and C 2. It is arched upward and backward dividing into two definite branches both of which undergo further subdivision. Ray B arises as a relatively thick continuation backward of the posterior medullary substance, giving off side branches and then dividing into three groups of terminal

branches which decrease in importance and extent from above downward. Ray A is a simple stem arising from the ventral aspect of the posterior medullary substance, proceeding downward and somewhat backward, giving off lateral branches.

The lobules

Lobulus 1 is a simple lingula formation consisting of three or four folia. Lobulus 2 is a rather subordinate lobulus divided into two portions and presenting five surface folia, the dorsal being more extensive than the ventral group. Lobulus 4 is subdivided into lobulus 4 A and lobulus 4 B, the entire complex presenting a marked similarity to the human type. Lobulus 4 A is a simple lobulus with a small number of surface folia which are subdivided into two groups. Lobulus 4 B is considerably more complicated in appearance and is subdivisible into at least three separate portions with a folial group of considerable size in the fissura primaria. Lobulus C is subdivisible into lobuli C 2 and C 1. Lobulus C 2 is a long, slender lobulus with an expanded summit, which raises itself to a considerable distance above the general outline of the arbor vitae and presents an extensive folial development in the fissures bordering the lobulus. Lobulus C 1 appears as a simple lobulus of five or six surface folia which are divided into two definite folial subgroups. Lobulus B is a relatively extensive lobulus, subdivisible into three portions, each presenting a simple serial group of folia. The upper group is a long, narrow lobulus presenting an extensive foliation, the middle group is simple and the ventral group consists of only a few folia. Lobulus A is small but rather wide, forming the caudal boundary of the fastigium.

The folial pattern of Simia satyrus

The orang-utan, in the arrangement of the cerebellar folia, presents an increasing similarity to the human cerebellum. The outline of the entire folial pattern is rounded and shows the even outline characteristic of the more advanced members of the primate order. The fissura primaria begins somewhat in front of the middle and passes outward and somewhat forward in an almost direct line. The fissura secunda appears between lobuli B and C and is continuous with a fissure which limits the caudal extremity of the lobulus paramedianus. The anterior lobe is much less extensive than the posterior lobe and presents an orderly disposition of its folia. Lobulus 1 is a lingual formation consisting of three vermal folia. Lobulus 2 presents a cephalic portion which is limited to the vermal region, while the caudal folia show an increasing tendency to extend farther and farther laterally. Lobulus 4 is subdivisible into two portions, lobuli 4 A and 4 B. Lobulus 4 A presents four folia in the midline, the cephalic two of which disappear in the fissure between lobuli 2 and 4 A. The other two are continued outward with the reappearance of one of the sunken folia. Lobulus 4 B is somewhat more complicated, showing a definite tendency to form a vermal ridge with lateral extensions. The folia in general are somewhat irregular in arrangement but extend outward throughout the width of the lobulus, the number, however, being somewhat reduced. All the folia of the anterior lobe show an increasing lateral disposition. Lobulus C presents three definite subdivisions: A cephalic portion shows a slight degree of vermal differentiation continuous with the long striplike folia which run the entire width

of the lobulus; this corresponds fairly well with the disposition of the lobulus simplex. The middle group arises from a small vermal origin, the very summit of lobulus C 2 in the arbor vitae, but spread laterally and assumes considerable proportions appearing to be crus 1 of the lobulus ansiformis. The caudal portion of lobulus C 2 presents a definite connection between the vermal and the lateral folia in its central portion, the folia of the cephalic and caudal portions tending to curl under and disappear into the sulci of the adjacent lobules and join the lower folia of the medullary ray. This part of lobulus C 2 may be homologized with crus 2 of the lobulus ansiformis. The caudal folia show a marked tendency to retract toward the midline, becoming much shorter and showing a tendency to the formation of a lobulus paramedianus. Lobulus C 1 shows a distinct differentiation between its vermal and lateral portions. The former are, however, directly continuous with the striplike folia which run outward and arrange themselves in series with the folia of the caudal half of lobulus C 2. These folia show a progressive tendency to shorten, and the terminal folia are folded underneath the more cephalic folia as a rapidly diminishing series, forming the concluding portion of the lobulus paramedianus. Lobulus B is a relatively extensive group of folia which presents a definite rosettelike form, the peduncle of which is continuous with the rudimentary group of folia which appear in the situation of the lobulus parafoccularis. The lobulus parafoccularis begins in the recess beneath the termination of the folial chain of lobulus C 1, as a group of folia which emerge on the surface and extend outward for a short distance in a simple serial arrangement of folia, without the formation of a peripheral rosette. Lobulus A presents a group of vermal folia in the formation of a rosette, the peduncle of which is merged with that of the medullary substance in the general direction of the lobulus floccularis. The lobulus floccularis presents the appearance of a simple folial rosette with a few terminal folia connected with the termination of the lobulus parafoccularis.

The insertion of the various lobules into the medullary substance does not present any definite characteristics except lobulus 1 which shows a definite peduncle. The remainder are inserted together in a continuous series throughout the entire cerebellum verging on the origin of the sulcus horizontalis magnus. A definite sulcus horizontalis magnus is discernible in the middle of the lateral extension of lobulus C 2 and it appears in the usual position of the sulcus intercruralis, crus 1 forming its cephalic lip, and the caudal margin being formed by the folia of crus 2.

Physical characteristics of Simia satyrus

— The orang-utan is an anthropoid ape, measuring from 3 feet 10 inches to 4 feet 6 inches in height, and is fairly heavy in its body structure. The head is large; the eyes are placed anteriorly, thus possessing overlapping fields of vision and showing conjugated movements of the eyeballs. The tongue is of moderate size and the ears are small and human in appearance. The neck is short, thick and freely movable. The arms are powerful and long, extending almost to the ankles in the erect position. The legs are short, thick and bowed. The fingers are webbed at the base, and the thumb is small. The foot is long and narrow, the great toe being short. The orang is entirely arboreal. It can progress clumsily

on the ground on all fours, using its arms as crutches and resting the sides of the feet only on the ground. In the trees it travels deliberately but with perfect ease, usually swinging along under the boughs, but at times walking on them in a semi-erect position. It can stand erect and has been seen to take a step unaided. It possesses great unilateral independence of the four extremities, the skill and finesse of movement being greater in the fore than in the hind limbs. They are essentially quadrumanal in organization. The hind limbs are not organized for locomotion. They are agile and capable of a high degree of training.

GORILLA GORILLA

The pattern of the arbor vitae of the gorilla is more or less irregularly round, there being a considerable deviation from the spherical form in the extension upward and backward of lobulus C 2. The fissura primaria is situated in the usual position, almost directly vertical, with its ventral extremity approaching the summit of the fastigium. These two structures divide the arbor vitae into a smaller anterior and a larger posterior lobe. The ventricular fastigium is rather narrow and fairly deep. The fissura secunda appears in the usual position between lobuli B and C directed from before somewhat backward and upward, dividing the lobe into a much smaller ventral and a much larger dorsal portion. The medullary substance is concentrated in the center as a large mass and is shared by both the anterior and posterior lobes without any definite demarcation. The arrangement of rays 4 and C produces a distinct U-shaped conformation in the vertical disposition of these branches as they arise from the medullary substance. The general appearance of the arbor vitae shows a distinct advance toward the human type in arborization, foliation and the special characteristics mentioned in connection with *Simia*.

The medullary rays

Ray 1 presents a structure which may be viewed as a compromise between a definite stalk arising from the medullary substance and a lingula in which the definitive medullary stem is usually lacking. It arises from the ventral aspect of the anterior medullary substance and is directed downward and slightly forward, presenting a moderate degree of secondary division, and at the same time is partially merged with a layer of gray matter lying on the superior medullary velum. Ray 2 is directed forward from the medullary substance as a slender branch which gives off lateral subdivisions and terminates in a bifurcated extremity. Ray 4 is a stout branch arising from the dorsal aspect of the medullary substance, proceeding somewhat forward and upward and giving off a heavy branch cephalically which forms a definite ray 4 A. The remainder of the stalk continues upward and forward and divides into two heavy branches, which undergo secondary division, and a terminal bifurcation. Ray C arises as an upward and backward prolongation of the entire posterior medullary substance, and divides into a cephalic ray C 2 and a caudal ray C 1. Ray C 2 which proceeds obliquely upward and backward gives off a number of heavy branches in the depths of the fissura primaria and a prominent cephalic branch. It divides to form the apical sublobules of lobulus C 2. There is a single strong process forming the caudal group of folia of lobulus C 2.

Ray C 1 arises near the base of ray C 2, and proceeds backward and somewhat upward, giving off a series of strong lateral branches. Ray B is a heavy ray below the center of the posterior medullary substance, proceeding backward and dividing into two groups of branches, the ventral of these again subdividing. Ray A is a heavy, thick stem from the ventral aspect of the medullary substance which proceeds downward and then almost directly backward giving off side branches of considerable size and importance.

The lobules

Lobulus 1 presents characteristics which cause it to appear as a modified lingula, possessing a definite stalk, with independent branches, and also a rather broad attachment to the superior medullary velum. It is fairly extensive, consisting of three surface folia. Lobulus 2 is relatively reduced and appears as a narrow lobulus composed of lateral folia and a terminal cluster. Lobulus 4 is subdivided into a cephalic lobulus 4 A and a caudal lobulus 4 B. Lobulus 4 A is a fairly narrow lobulus proceeding straight forward and composed of lateral serial folia. The apex is somewhat widened and presents a series of single folia. Lobulus 4 B is extensive and appears like the human lobulus 4 B through the turning backward of the apical medullary ray. It is irregular in shape and is composed of two rather extensive folial groups. The cephalic group presents the usual lateral folia and a surface group which is subdivided into a smaller cephalic and a larger caudal cluster. The main caudal divisions of lobulus 4 B present a rounded summit with an extensive series of folia in the fissura primaria. Lobulus C is almost quadrilateral and is subdivided into a much larger lobulus C 2 and a small lobulus C 1. Lobulus C 2 is a considerably expanded group of folia which shows a distinct resemblance to the human type. There is a series of relatively extensive folia in the depths of the fissura primaria. The surface folia are divided into a series of folial groups at least five in number, the cephalic group being the most conspicuous. This arrangement is similar to the type found in the cerebellum of the chimpanzee and that of the human being. The caudal group is distinct and separate. Lobulus C 1 is long and narrow, formed by lateral serial folia and presenting two small groups of surface folia. Lobulus B is extensive, beginning as a narrow structure but rather rapidly expanding into a bulbous termination formed by three folial subgroups, the dorsal and ventral divisions being rather simple and the middle one more complicated. Lobulus A appears as an elongated curved lobulus which lies under cover of lobulus B.

The folial pattern

The folial pattern also shows a distinct advance in the configuration and organization of the cerebellum as it approaches its morphologic consummation in man. The fissura primaria is situated only a little in front of the center of the folial pattern and is continued outward and forward to the periphery. The fissura secunda appears in the usual position between lobuli B and C and caudally limits a group of lateral folia which are distinctly in the paramedian position. The anterior lobe is progressively occupying less and less of the hemispherical surface. Lobulus 1 presents two vermal folia and a third which presents a definite lateral

extension. Lobulus 2 is relatively reduced and presents definite vermal and lateral portions and consists of five vermal folia which are reduced to three at the periphery. Lobulus 4 is subdivided into a simple cephalic portion corresponding with lobulus 4 A and a much more extensive lobulus 4 B. Lobulus 4 A presents definite vermal and lateral portions. Lobulus 4 B is more complicated in its arrangement, several folia appearing from the depths and maintaining themselves on the surface, while a considerable number of folia disappear by joining adjacent sulci. The lobulus does not present any definite diminution in size as it approaches the periphery. The vermal differentiation is clearly to be seen, being irregular, while the lateral striplike

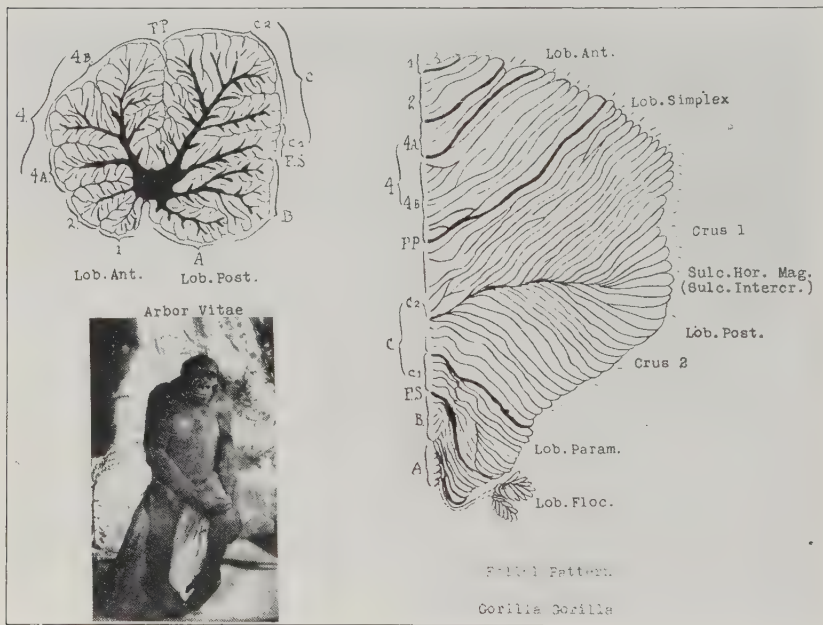


FIG. 37. *Gorilla gorilla*

folia are much more regular. Lobulus C presents a cephalic portion, lobulus C 2, which is subdivisible into a number of independent portions. The most cephalic folia present a relatively simple arrangement extending from the midline to the periphery. These may be considered the folia of the lobulus simplex. The next succeeding group tends to become shorter and shorter as the folia proceed outward, forming a definite intercrural sulcus with an apex, thus comprising a fairly definite crus 1. The succeeding folia return toward the midline, and as these terminate mesially in the same sulcus they form crus 2. These two groups of folia may be considered to constitute the lobulus ansiformis. The folia continued backward, the most caudal becoming continuous with the last of the vermal folia of lobulus

C 2. The intercrural sulcus presents a considerable degree of similarity in position and in character to the sulcus horizontalis magnus. The folia of lobulus C 1 present vermal portions which show definite connections through the paramedian sulcus, in the case of the cephalic folia directly with the lateral group of folia forming the lobulus paramedianus, and in the case of the caudal portion indirectly by means of a broad peduncle which joins the caudal continuation of the lateral folial chain forming the lobulus paramedianus. The lobulus paramedianus directly follows the most caudal folia of crus 2 as a series of narrowing folia. The most cephalic of these are directly continuous with the cephalic folia of lobulus C 1. The caudal folia continue to shorten laterally and mesially and are attached to a broad peduncle which is continuous with the submerged folia of lobulus C 1. Lobulus B presents a group of vermal folia provided with a definite peduncle which is continuous with the folial mass forming the caudal extremity of the folial chain of the hemisphere. These folia are not arranged so definitely in a tonsillar form as those of the chimpanzee, the caudal folia presenting a distinctly infolded arrangement, and they do not appear on the surface but are connected with the folia submerged in the fissure between lobulus B and lobulus A. The lateral folia, being connected with lobulus B, represent the lobulus parafoccularis. They do, however, present an appearance strikingly similar to the tonsil of the chimpanzee and of man. The remnants of this infolded arrangement of the terminal folia of the lobulus parafoccularis can be discerned in the caudal folia of the tonsil of man.

Lobulus A presents a group of simple vermal folia drawn into a peduncle which joins the medullary substance. The lobulus floccularis lies laterally and consists of a double group of folial rosettes situated between the cerebellar peduncle and the lateral surface of the lobulus paramedianus.

The implantation of the lateral portions of the hemisphere into the medullary substance presents a simple row of direct folial implantations into the medullary substance without the interposition of definite peduncles. These form the groups of folia that make up the superior and inferior margins of the hilum of the cerebellum and are continuous outward into the bottom of the sulcus horizontalis magnus, which, in the gorilla, seems to be directly homologous with the sulcus intercruralis.

Physical characteristics of Gorilla gorilla

The gorilla is of great size and strength. The head is massive; the eyes are situated anteriorly, possess overlapping fields of vision and are well conjugated in their movements. The ears are human in their appearance, and are only slightly movable. The tongue is small. The neck is extremely heavy and freely movable. The tail is rudimentary. The extremities are of unequal length, the arms being considerably longer than the legs and reaching to the midcalf. The hands are thick and clumsy, the thumb is short and freely functioning and the fingers are joined at their bases by a web. The lower extremities are relatively short and stocky, the leg being quite short. The toes are short and stumpy, and the great toe has more the appearance of a thumb. It is almost entirely terrestrial in habitat, although it can climb trees. In walking, the animal places the dorsal surface of the fingers on the ground, the body being brought forward with a swinging

half-jump. The gorilla can stand and walk erect and it seems to assume this posture when in the aggressive. When captured young, it is capable of great training and can use its hands and feet in performing acts of great delicacy and dexterity. The quadrumanal type of organization has deferred the perfect specialization of the feet as the organ of locomotion, and the hand is the explorer of the environment.

ANTHROPOPITHECUS TROGLODYTES (CHIMPANZEE)

The pattern of the arbor vitae of the chimpanzee shows a marked similarity to that of the human being in the disposition of the medullary substance and the development of lobules 4 and C 2. In outline, it is more or less circular, with a rounded irregularity produced by lobules 4 and C 2. The fissura primaria is situated almost in a vertical line, somewhat cephalad of the middle, dividing the arbor vitae into a smaller cephalic and a larger caudal portion. The termination of the fissura primaria directly approaches the summit of the ventricular fastigium, which reaches the medullary substance. The fissura primaria and the ventricular fastigium together divide the arbor vitae into the anterior and posterior lobes. The fissura secunda appears somewhat below the middle of the posterior lobe, passing almost directly backward and somewhat above the general level of the medullary substance. The medullary substance is disposed as a markedly concentrated mass of white matter in the center of the arbor vitae between the termination of the fissura primaria and the ventricular fastigium. It appears as a small quadrilateral mass of medullary substance, giving origin to a number of lesser branches and two heavy dorsal prolongations, ray 4 and ray C. The arborization of the medullary tree is rich, and the resulting foliation is extensive. All the primary medullary rays are well defined, and the secondary branches are prominent. The arbor vitae is strikingly similar to the type found in human beings—more so than that shown by any of the other primates, and it could easily be mistaken for the human pattern. This similarity is particularly marked in the general appearance of the cerebellar section, in the form of the medullary substance, in the shape of the medullary rays 4 A and C 2 and in the general inclination of the medullary substance. The one striking dissimilarity is the lack of a definite lingula.

The medullary rays

The suggestion of a lingula formation is incorporated with the base of the first branch from the medullary substance which, therefore, must be called ray 1. This arrangement is not so marked as it is in the gorilla. Ray 1 arises as a direct downward extension of the anterior medullary substance and curves forward, giving off lateral branches. Ray 2 arises as a direct cephalic prolongation of the medullary substance, giving off lateral branches and subdividing into two definite stems. Ray 4 arises from the dorsal and cephalic aspect of the anterior medullary substance and is a stout stem, directed upward and forward, giving off a submerged branch in the sulcus between lobuli 2 and 4. It subdivides into an extensive series of cephalic branches and a relatively rich apical spray. There are a number of caudal branches in the depths of the fissura primaria. The secondary and tertiary subdivision of the ray is rather extensive, producing a rich foliation in the formation of

lobulus 4. Ray C arises as a direct continuation of the entire posterior medullary substance in a more or less oblique fashion, from before backward and upward. The primary stalk is a thick heavy stem which gives off lateral subdivisions and then divides into two portions; a cephalic portion, ray C 2, extends upward and forward, giving rise to a number of cephalic and caudal divisions, and at its termination produces a spray of branches which form the summit of the lobulus and are similar to those of the cerebellum in human beings. There are two small branches which lie in the depths of the fissure between lobuli C 2 and C 1. Ray C 1 arises

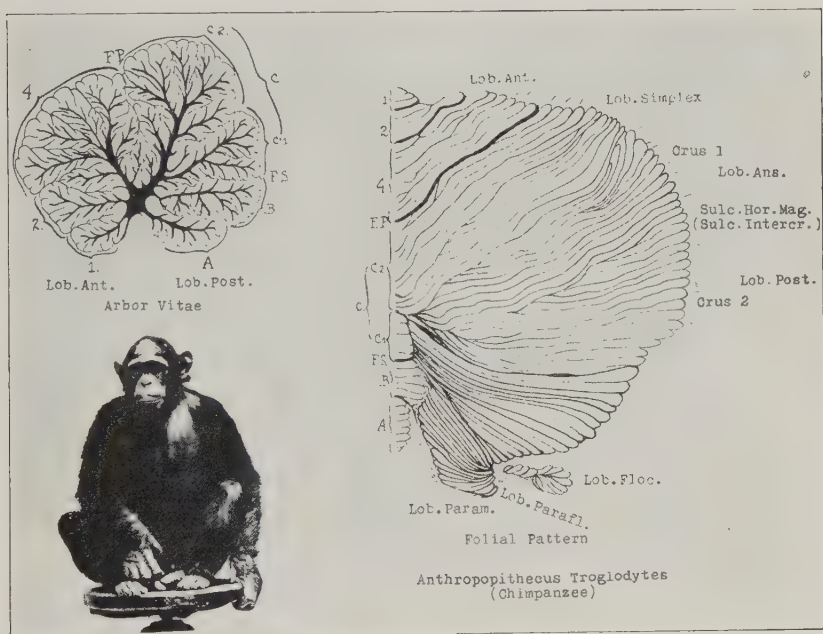


FIG. 38. *Anthropopithecus troglodytes* (chimpanzee)

from the lower and caudal part of ray C, gives off an extensive series of lateral branches and then divides into two rather extensive rays which present a considerable degree of subdivision, the dorsal stem undergoing an extensive terminal branching. Ray B arises from the caudal aspect of the posterior medullary substance, proceeds directly backward, giving off rather richly branched rays, and subdivides. Ray A is a rather heavy process from the posterior medullary substance close to the ventricular fastigium which proceeds almost directly backward, giving off lateral branches.

The lobules

Lobulus 1 is fairly extensive, and would be incorporated in lobulus 2, if the abortive lingula formation had been somewhat further developed. It consists of a single folial cluster. Lobulus 2 is a narrow folial group consisting of dorsal and ventral laminae. The bifurcation of the medullary ray produces two groups of surface folia. Lobulus 4 is complicated; it is subdivided into four groups of surface folia, a submerged folial group in the fissure lying between lobuli 2 and 4 and a diminishing series of folial groups which form the cephalic margin of the fissura primaria. The four groups of surface folia are relatively simple and form a rounded eminence extending above the general surface of the arbor vitae. Lobulus C forms by far the major portion of the posterior lobe and is subdivided into an extensive lobulus C 2 and a smaller lobulus C 1. Lobulus C 2 presents a number of folial groups which form the caudal wall of the fissura primaria. Its apex is formed by a group of surface folial clusters which extend upward above the general surface of the arbor vitae as does lobulus 4. It is strikingly similar to the human type, except that the apical folial group which in man forms the folium cacuminis is not quite so extensively developed. The same submerged folial group which in man is found to be connected with the most caudal of the folia of the lobulus tuberosemilunaris (crus 2) is also present in the depths of the fissure separating lobuli C 2 and C 1. Lobulus C 1 is fairly extensive and is divided as in man into two definite portions. Lobulus B is well developed and presents two surface folial groups which are practically identical with their homologues in the cerebellum of a human being. Lobulus A forms a well defined caudal wall of the fastigium, similar to the human type.

The folial pattern of Anthropopithecus troglodytes

The chimpanzee possesses a folial pattern which is similar to that of human beings, manifesting a considerable advance over the pattern presented by gorilla. The fissura primaria is situated well forward, separating a small anterior lobe from a voluminous posterior lobe, the major portion of which arises as the result of an extensive development in lobulus C 2. The fissura secunda appears between lobuli B and C and can be traced outward into the lamellar chain between the caudal extremity of lobulus C 1 and the lateral extension of lobulus B which is organized on the plan of the human lobulus tonsillar. Lobulus 1 consists of a cephalic vermal folium and two caudal folia which show a slight tendency to expand laterally. Lobulus 2 is a relatively small group of folia, the cephalic lamellae being short while the terminal folium is relatively extended, showing a definite subdivision into a subdivided vermal and a single lateral portion. Lobulus 4, in contrast to its extensive development in the arbor, is rather small, presenting a definite vermal portion and a lateral division. The vermal sulci show a marked tendency to disappear in sulci which lie in front of them. The lateral folia are rather simply arranged as striplike lamellae; the cephalic laminae are somewhat irregular, but the caudal folia are long, narrow lamellae extending from the vermis to the periphery. The folia of lobulus C 2 divide themselves in general into two divisions, a cephalic which may be taken to correspond with the lobulus simplex and

a caudal division consisting of rather straight folia, which show a definite differentiation from the preceding folia, with a tendency for the caudal folia to disappear under cover of the more cephalic divisions of the lobulus, with the formation of what may be considered to be a sulcus intercruralis. This sulcus shows many of the characteristics of the human sulcus horizontalis magnus. The folia succeed one another, the orderly arrangement being interrupted in several regions by the appearance from the larger sulci of numerous folia which have extended outward from the deeper lamellae of the arbor vitae and gained a place on the surface. This accounts for the greatly expanded surface area of the folia of lobulus C 2 in the hemisphere. The folia which lie cephalad to the sulcus intercruralis represent crus 1. The folia of crus 1 are short at the beginning, rapidly extend in lateral disposition and then shorten as the apex of the ansiform formation is approached. The returning series of folia representing crus 2 gradually increase and then decrease in extent as the transition into the lobulus paramedianus begins, their mesial extremities being hidden beneath the more cephalic folia as they seek the submerged lamellae of the caudal portion of lobulus C 2 in the arbor vitae. Lobulus B appears as a well defined group of vermal folia presenting a rosette formation. It is clearly defined from its lateral derivatives by a fairly deep paramedian sulcus. The peduncle of the rosette rapidly expands and is continuous with an extensive group of folia which conclude the lateral chain, except for the lobulus floccularis. The folia of this expanded lateral portion of lobulus B may be homologized with the folia of the lobulus parafoccularis, although all of the characteristics of the lobulus parafoccularis of the subprimate representatives have been lost. The folial chain, as it approaches its termination, becomes rapidly reduced. Lobulus A is a relatively extensive group of vermal folia which form a rosette. The ill defined peduncle loses itself in the medullary substance. The lateral portions of this lobulus, the lobulus floccularis, present a short series of folia which expand into a rather prominent rosette.

The implantation of the various portions of the folia into the medullary substance is quite human in its arrangement. The implantation takes place along the lips of the sulcus horizontalis magnus as that structure arises at the hilum of the cerebellum and extends outward to become continuous with the sulcus intercruralis. The folia which reach the medullary substance along the dorsal lip of the sulcus horizontalis magnus are implanted separately, without the intervention of any peduncular formation. The folia of the caudal lip present a similar arrangement.

Physical characteristics of Anthropopithecus troglodytes

— The chimpanzee is a heavily built animal and is the most human of all the apes in appearance. The head is large; the eyes are situated anteriorly, thus possessing overlapping fields of vision, and are well conjugated in their movements. The ears are large, rounded and somewhat movable. The neck is short and heavy, and presents a free range of movement. The tail is rudimentary. The extremities are not so long as they are in the lower monkeys, the arms extending only to about the knee. Both the hands and the feet are rather long. The hands are well developed, the thumb being freely functioning, and the fingers are joined at their bases by a web. The toes are long, about as long as the fingers. The big toe

arises at a considerable angle and resembles the thumb. The chimpanzee is able to stand and walk upright, but not so extensively as the gorilla. It prefers to proceed with the back bent forward, the body being supported by the fore limbs, with the fingers close in the palm so that the knuckles are in contact with the ground. The chimpanzee spends some of its life on the ground, but it is more arboreal than the gorilla. It is highly intelligent and imitative, and can be taught many skilled acts requiring great manual differentiation. It can use its fingers and, to a less extent, its toes, with almost human finesse and dexterity. The manual differentiation of the feet has retarded the assumption of the erect posture and postponed the division of labor, which destines the feet for locomotion and the hands and fingers for the organization of skilled movement, the characteristic of human manual development.

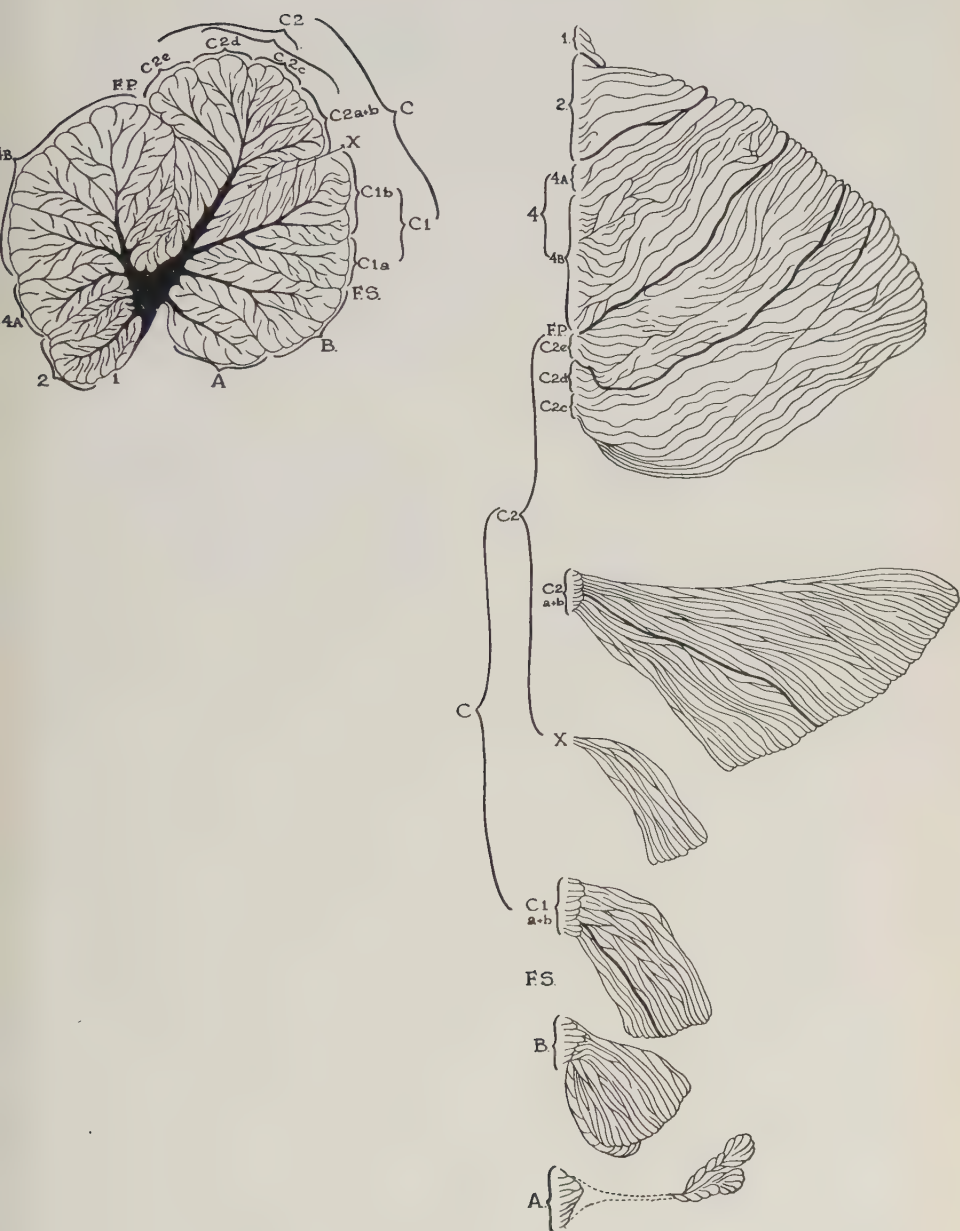
HOMO SAPIENS (MAN)

The form of the arbor vitae of man is more or less rounded, with a distinct surface elevation produced by lobulus C 2. The fissura primaria appears somewhat in the advance of the middle of the cerebellum and proceeds downward and backward, and then directly downward, to approach the summit of the ventricular fastigium which is rather triangular in shape. The fissura primaria and the ventricular fastigium separate the arbor vitae into a smaller anterior and a larger posterior lobe. The fissura secunda appears in its usual position between lobuli B and C. It lies almost directly horizontally and is situated a little above the level of the medullary substance. It subdivides the posterior lobe into a larger dorsal and a smaller ventral portion.

The medullary substance appears as a more or less triangular mass of white matter, and is disposed in a peculiar oblique direction from before backward and upward. The major portion of the medullary substance is situated cephalad to the line joining the bottom of the fissura primaria and the summit of the ventricular fastigium, and therefore lies chiefly in the anterior lobe. The medullary substance of the anterior lobe forms a triangular mass from which arise the medullary rays, and from its caudal extremity the medullary substance of the posterior lobe is continued upward. The marked continuation of the medullary substance downward into the superior medullary velum and backward and upward into C 2 causes the peculiar oblique disposition of the entire medullary mass. The branching of the medullary tree is extensive, particularly in the production of the smaller stems, so that the foliation is delicate and voluminous. In man, lobulus C 2 reaches its acme of development.

The medullary rays

Ray 1 appears as a definite lingula formation with the extension of the medullary substance into the superior medullary velum surmounted by a simple group of folia. Ray 2 consists of the branches which arise directly from the cephalic aspect of the anterior medullary substance. The first stalk is a relatively heavy stem which proceeds downward and forward, giving off a large number of lateral branches. The second branch is a lighter stalk, rising dorsal to the first medullary branch, which gives rise to a considerable number of lateral derivatives. There

FIG. 39. *Homo sapiens* (man)

are also one or two small branches arising from the medullary substance independently. Ray 4 appears as the principal offshoot from the anterior medullary substance and arises as a thick stem from the apex of the central white matter, extending upward and somewhat forward. Ray 4 gives off close to its origin, a stout cephalic branch which subdivides the lobule into lobuli 4 A and 4 B. The rest of the stalk proceeds upward and forward, giving off several cephalic branches and a number of more slender caudal branches which lie in the depths of the fissura primaria. It terminates by dividing into a group of rays which present a considerable degree of secondary and tertiary subdivision. Ray C arises as a direct continuation and prolongation of the posterior medullary substance in the form of a thick stem directed upward and backward which divides into a relatively heavy branch, ray C 2, and a more slender branch, ray C 1. Ray C 2 is a direct continuation upward and backward of ray C, which gives off a number of lateral subdivisions and ends in a rich terminal spray of five rays which proceed cephalically, dorsally and caudally. These undergo a considerable resubdivision and contribute the characteristic development of the human cerebellum giving attachment to the enormous mass of lateral folia which is connected with the apical folial spray. One of the caudal branches is designated as ray X. Ray C 1, the caudal division of ray C, arises as a more slender stem than ray C 2, proceeds upward and backward, giving off a considerable number of slender dorsal branches and a pair of definite ventral branches, and ends in a limited spray of secondary branches. The first considerable ventral branch is ray C 1a, while the continuation of C 1 becomes ray C 1b. Ray B arises as a simple stem from the caudal aspect of the posterior medullary substance, gives off a few lateral branches and divides, the derivatives giving rise to a number of smaller branches. Ray A is a rather definite stalk, arising from the medullary substance immediately above the ventricular fastigium, directed obliquely backward and downward and giving off a few subsidiary lateral branches.

The lobules

Lobulus 1 consists of a few folia which are supported directly by the superior medullary velum and thus form the lingula. The group of folia which constitute lobulus 2 is subdivided into two parts, a ventral portion which is more extensive, with a closely set series of lateral folia, and a smaller dorsal collection. These two groups together compose the lobulus centralis. The remainder of the anterior lobe is made up of lobulus 4, which is called the culmen monticuli. The culmen monticuli, or lobulus 4, is roughly quadrilateral in form and is primarily subdivided into two folial groups, lobuli 4 A and 4 B. Lobulus 4 A is developed by the origin of a principal cephalic subray, ray 4 A. It is a narrow folial cluster, composed of serial lateral folia, with a surface subdivision into two smaller sublobules. Lobulus 4 B comprises the remainder of lobulus 4 and is made up of five separate sublobules. The first is rather triangular in shape, its base being located on the surface, and is subdivided into two folial groups. The remainder or deep part of the sublobulus is made up of lateral serial folia. The second sublobulus is somewhat similar in arrangement to the preceding but is less highly organized. The third sublobulus forms the summit of lobulus 4, is triangular in shape and

presents three surface subdivisions. The fourth and fifth sublobules are of diminishing size and form a part of the cephalic wall of the fissura primarius. Lobulus C 2 presents a complicated subdivision and is roughly quadrilateral in outline, its dorsocaudal angle being rounded off, providing the characteristic feature of the human cerebellum. There are a number of folial groups which form the caudal wall of the fissura primaria, two of which are of greater extent than the remainder. The first group of folia of lobulus C 2 which appears on the surface forms a series of three or four folia, constituting the clivus monticuli, sublobulus C 2e. The next subdivision comprises the terminal branching of ray C 2 and appears as two groups of surface folia, sublobulus C 2d and C 2c. These together form the folium cacuminis. The concluding groups of lobulus C 2, lobuli C 2b and C 2a forming the caudal folial clusters of lobulus C 2, together constitute the tuber valvulae, although they arise as separate stems from the upper part of ray C 2. A submerged folium is designated as sublobulus X. Ray C 1, subdividing rather extensively, gives rise to at least two sublobules—lobulus C 1a and lobulus C 1b, which together form lobulus C 1, the pyramis, which is triangular in shape. Lobulus B is also triangular in form, with a deep portion made up of serial folia and a superficial division made up of two folial clusters. The combined lobulus is called the uvula. Lobulus A forms the caudal margin of the fastigium and is a simple lobulus made up of dorsal and ventral folia. It is called the nodulus.

The folial pattern of the human cerebellum

In describing and naming the lobules and fissures appearing in the folial pattern, a great deal of confusion arises on account of the folded arrangement of the cerebellum by which fissures and sulci which are really caudal in derivation become situated anatomically in front of their morphologic antecedents. With the folial pattern laid out in one plane, the terms cephalad and caudad possess their own essential significance. The folial pattern of the human cerebellum is divided by the fissura primaria into a much less extensive anterior lobe and a much larger, more complicated and highly organized posterior lobe. The fissura secunda appears between lobuli B and C and is continued outward separating the lobulus paramedianus from the lobulus parafl occularis corresponding with the lobulus pyramidobiventricis and the lobulus uvulatonissillaris. Lobulus 1 corresponds with the lobulus vinculolingualis and is limited by the fissura prelingualis cephalad and the fissura precentralis (centrolingualis) caudad. It is composed of a small number of folia supported by the superior medullary velum. Lobulus 2 presents a considerable degree of folial differentiation with a definite division into vermal and lateral portions. The lateral folia are fairly regular in this distribution, rather extensive and reach well out into the hemisphere. The number of vermal folia is considerably in excess of those which reach the periphery. Lobulus 2 corresponds with the lobulus centro-alaris bounded by the fissura precentralis (fissura centrolingualis) cephalad and the fissura prelunata (fissura culminocentralis) caudad. Lobulus 4 is subdivided into a cephalic subsidiary portion, lobulus 4 A, and a much larger caudal portion, lobulus 4 B. Lobulus 4 A presents a definite vermal differentiation with a pair of small lateral folia which run outward but do not reach the periphery. The remainder of the lobulus, lobulus 4 B, is made up of

rather complicated groups of folia which run in an irregular fashion, in general, however, laterally. In several places the folia are irregular, intersecting the general lateral disposition of the lamellae. Numerous laminae appear and disappear into the sulci bounding the lobulus, and many of the sulci appear, run for short distances and disappear. The representation of this lobulus at the periphery is much less than that at the midline. Lobulus 4, the lobulus culminolunatus is composed of the culmen monticuli and the anterior lunate lobule, and is limited cephalad by the fissura prelunata (fissura culminocentralis) and caudad by the fissura superior anterior (fissura declivoculminalis).

Lobulus C is subdivided into a number of vermal and lateral portions. From before backward, the first vermal portion C 2e corresponds with the clivus monticuli and, with the lateral extensions which form the posterior lunate lobule, comprises the lobulus declivolunatus. The lobulus declivolunatus, on account of its position caudad to the fissura primaria, is homologous with the lobulus simplex. It is bounded cephalad by the fissura superior anterior (fissura declivoculminalis) and caudally by the fissura superior posterior (fissura foliodeclivalis). The lobulus is derived from a rather narrow origin from the arbor vitae and immediately extends caudally by the addition to it of folia which appear from the fissura superior posterior. The folia tend to run at first caudally and then to swing laterally, there being a tendency for the lobulus to break up into two folial groups, both of which are rather irregular. The caudal subdivision appears from the depths of the fissura superior posterior, the folia running rather irregularly toward the periphery. The two succeeding groups of vermal folia, C 2d and C 2c, are combined as the folium cacuminis. Folium C 2d is extensively represented in the vermis, but in the lateral portion of the lobulus, the folia disappear and reappear, the vermal and lateral portions apparently being connected together in the depths of the fissura superior posterior. The intermediate portion of the lobulus presents parallel sulci which, however, run obliquely across the surface of the lobule, disappearing in a secondary fissure which crosses its surface, the lobulus becoming narrower as the periphery is approached. The caudal portion of the lobulus presents a diverging series of folia which appear from under cover of the preceding folial group and continue to increase in size to the periphery, producing a distinctly triangular subdivision. These folia may be homologized with the folial arrangement of crus 1. The lateral folia tend to be arranged diagonally across the lobulus. The combined lobulus is composed of the central vermal constituent, the folium cacuminis and the hemispherical constituent, the anterior semilunar lobule, also called the posterior superior lobule. The entire lobulus is called the lobulus folioseminularis and is bounded cephalically by the fissura superior posterior (fissura foliodeclivalis) and caudally by the fissura horizontalis or the sulcus intercruralis.

On account of the difficulty in presenting the form of the cerebellum with the vermal folia following one right after the other in an interrupted series, the independent vermal groups and their lateral extensions are separated in the diagram. The group of folia representing C 2a and C 2b, the lobulus tuber valvulae, is connected with an extensive series of lateral folia which present a much greater peripheral than vermal distribution, there being a distinct paramedian sulcus between the two divisions. There is a distinct vermal condensation in the number of folia. This lobulus presents a tendency for the folia to run into the fissure bounding it

superiorly, therefore homologizing it with crus 2. The folia progressively diminish in lateral extent and show a tendency to be segregated into two subdivisions. This lobulus is called the lobulus tuberosesemilunaris and is limited cephalad by the fissura horizontalis (fissura tuberosfolialis) or the sulcus horizontalis magnus, the counterpart of the sulcus intercruralis. The lobulus is composed of the tuber valvulae and the lateral extension, the posterior semilunar lobule, which is also called the posterior inferior lobule.

The next group of folia represents a structure in the lateral hemisphere produced by the emergence of a group of submerged folia, which is marked "X" in the arbor vitae. This is an integral part of lobulus C 2a and C 2b, the folia succeeding the lobulus tuberosesemilunaris as a diminishing series of folia. Lobulus C 2 is limited caudally by the fissura inferior posterior (fissura pyramidotuberalis).

Lobulus C 1 consists of a double group of vermal folia, lobuli C 1a and C 1b, and shows a definite paramedian sulcus through which the folia are continuous with a series of lateral folia which proceed outward and then caudally forming the lobulus pyramidobiventricus. By reason of its vermal associate in the arbor vitae and its form and position in the hemisphere it represents the lobulus paramedianus. This lobulus is limited cephalad by the fissura inferior posterior (fissura pyramidotuberalis), and caudally by the fissura inferior anterior (fissura uvulapyramidalis).

Lobulus B represents a group of vermal folia, disposed in the form of a typical roset, drawn out into a contracted peduncle which expands markedly into a large group of folia that form the tonsil. These folia show a marked tendency toward infolding above and below, so that a narrow neck is produced which expands into a large group of folia that appear in direct continuation with the lobulus paramedianus. Under cover of its caudal portion, a number of folia run outward in a series to end in a blunt extremity completely overlain by the caudal folia of the tonsil proper. This lobulus is called the lobulus uvulatonsillaris, limited cephalically by the fissura inferior anterior (fissura uvulapyramidalis), and caudally by the fissura preuvularis (fissura nodulo-uvularis). On account of its position and particularly its connections, the lobulus uvulatonsillaris may be homologized with the lobulus parafoccularis.

Lobulus A appears as a group of vermal folia forming a definite rosette and a peduncle which appears to extend outward toward the region of the flocculus. The flocculus consists of a double rosette, each part of which is terminated by a chain of folia. This is the lobulus nodulofloccularis. The lobulus nodulofloccularis is bounded cephalically by the fissura preuvularis (fissura nodulo-uvularis), and caudally by the fissura prenodularis (fissura nodiolonodularis).

Physical characteristics of Homo sapiens

Man presents a body adapted to an upright position. The head is rounded, the eyes are situated anteriorly, thus possessing overlapping fields of vision, and they present perfect conjugation in movement. The lips, tongue and cheeks present a marked degree of differentiation in conjunction with the larynx, respiratory muscles, etc., in the function of speech. The neck is of moderate length, and is freely movable. The trunk is of moderate size and weight. The upper and lower

extremities are of about equal length. The upper extremities are completely freed from the necessities of locomotion and present the culmination in manual dexterity. The lower extremities which are in direct line with the trunk are used chiefly for locomotion but have a marked degree of unilateral independence and are capable of a high degree of training. Man represents the final bimanual development, with a monomanual predominance, which has resulted from the specialization of the foot as the agent of support and locomotion and the freeing of the upper extremities from these necessities.

COMMENT

A definite attempt at functional localization in the cerebellum on the basis of this study is impossible. The number of forms is too small, and the distinct differences in the cerebellum are too slight to be singled out with any degree of certainty. It seems definite, however, that the size of the cerebellum and the complexity of foliation is largely dependent on the corporeal bulk of the animal. In comparing the various cerebella in regard to the degree of complexity and of functional development which they present, it seems clear that the most simply organized cerebellum which has been encountered in this series is that of *Bradypus tridactylus* in which almost the entire cerebellar development is axial, all of the folia being transversely arranged, practically equivalent in size and without any material development of the lateral outgrowths which characterize the cerebellum in the other forms. Many of the cerebella are smaller, particularly those of the rodents, the bat, the lemur and the marmoset, but in all of them there is an expansion and development, particularly in the region of lobulus C, which is only faintly suggested in the cerebellum of *Bradypus*. The reason for this is not difficult to determine and is due to the peculiar bodily conformation and physical constitution of the sloth which spends almost its entire life in a pendent position from the limb of a tree. Its means of progression are rudimentary and there is, to all intents and purposes, no unilateral independence of the fore and hind limbs. The sloth is scarcely able to drag himself along the ground and rarely leaves his characteristic suspended position.

The most complicated cerebellum is that which corresponds to the animal which possesses the greatest bulk, that is, the elephant. Closely approaching the cerebellum of the elephant in the degree of complexity comes that of the narwhal. In clearcut definition and evident convolutional organization, the primate series, and in particu-

lar *Homo sapiens*, presents interesting examples of regional development and suppression in the organization of the cerebellum.

THE PARAVERMIS

The cerebellum of the ungulates presents a typical and characteristic development. These animals require a considerable increase in cerebellar synergic activity through their greatly increased bulk, their long mobile necks and trunks and their long legs. These requirements chiefly affect the axial musculature, and the cerebellum answers this increased demand apparently by an expansion in its median portion, the vermis. This influences the entire vermis, but particularly that part which is in connection with lobulus C and lobulus B, and results in what really amounts to a paravermis through the extreme side-to-side convolution of the vermal folial chain. This is clearly evident in the elephant, the camel, the giraffe and, to a certain extent, the calf. In these animals, the complexity of development of the median portion of the cerebellum far exceeds that of the hemisphere.

ANATOMIC HOMOLOGIES OF THE HUMAN CEREBELLUM

In regard to any effort to homologize the lobes and lobules of the human cerebellum with those of the comparative series, all investigators who have studied this question have emphasized the futility of attempting to establish a direct connection between the various lobes and lobules of the human cerebellum with the divisions and subdivision of the cerebellum as seen in the mammalian group. From the results of this study, as far as it has been carried, this is entirely true functionally, but anatomically the various lobes and lobules of the cerebellum seem to be arranged according to the same general plan as that presented by the entire comparative series from the point of view both of the arbor vitae and of the folial pattern. These homologies are apparently corroborated by the facts of embryologic development, particularly in regard to the relationship established between the vermal and hemispherical constituents of the caudal end of the folial chain, that is, the pyramis and the biventer, the uvula and the tonsil and the nodulus and the flocculus. The gradual reduction of the paraflocculus throughout the primate series is easily traceable to its remnant in *Simia*, *Anthropopithecus* and *Gorilla*.

THE SULCUS HORIZONTALIS MAGNUS

One of the conclusions in regard to the primate cerebellum which seems to establish itself definitely is the identification of the sulcus horizontalis magnus with the sulcus intercruralis of the lobulus ansiformis. These sulci both develop in the hemispherical expansion connected with lobulus C 2. The organization of the sulcus formed by the approximation of the mesial extremities of the folia of crus 1 and crus 2 is easily followed in the more simple types of cerebellar crystallization and definitely establishes itself in the ungulate and carnivorous types. This ground plan is easily recognizable in the lower and intermediate primates. As the foliation of the hemispherical portions of lobulus C 2 become richer when the higher primates are reached, a gradual transition takes place into the configuration of the sulcus horizontalis magnus as seen in the gorilla and the chimpanzee. In man, the great horizontal sulcus occupies the identical position held by the sulcus intercruralis in the lower forms, and a definite reminiscence of crus 1 and crus 2 can be made out in the arrangement of the folia forming the fissure.

LOCALIZATION IN THE ANTERIOR LOBE

According to the investigations of Bolk, André-Thomas, Durupt, Van Rijnberk and others, the various lobules of the anterior lobe have received definite synergic allocations as follows: the eye movements in lobulus 1, the lingual musculature in lobulus 2, the masticatory movements in lobulus 3 and the combination of the mimetic musculature and the activity of the laryngeal and pharyngeal muscles in lobulus 4. In a consideration of lobulus 1, the chief variation noted is in the rather extensive development of this lobule in the arbor vitae of the ungulates. This development is not carried to any extent in the hemisphere. In these animals, the eyes are placed in the lateral aspects of the head, and the direction of gaze is largely controlled by the position of the head. In the other suborders, the lobulus is fairly uniform, and a definite expansion cannot be identified in the animals in which the eyes are placed cephalically and in which the synergic control of the eyes has developed to such an extraordinary extent as that shown by the higher anthropoids and man. Lobulus 2, to which is allocated the synergic control of the lingual musculature, is highly developed in all the lower forms, such as the marsupials and the

ungulates. It is fairly well developed in *Fissipedia* and considerably more highly specialized in *Pinnipedia*. It is prominent in the lower primates, then rapidly diminishes in the higher anthropoids finally to gain a considerable degree of development in man. Lobulus 3, to which is assigned the synergizing of the masticatory movements, is so variable that it is difficult to arrive at any definite conclusions in regard to its particular control. When it is present its origin and the disposition of its lateral extensions would align it more with lobulus 4 than with lobulus 2, and when it is absent there are branches of ray 4 which suggest that it had been incorporated with lobulus 4. The only suborder in which it presents any degree of constancy is the rodents, and this would scarcely add any plausibility to the hypothetic functions assigned to it.

In regard to lobulus 4, it is difficult to believe that the synergic needs of the facial, laryngeal and pharyngeal muscles should require such an important subdivision of the cerebellum. It is only in the carnivora and the primates that the mimetic musculature has arrived at any degree of differentiation. The synergic necessities of the larynx and pharynx are only moderately advanced in the lower forms, and the human cerebellum does not show the degree of expansion which would be expected if this lobule should govern the vast range of facial expression and the infinitely fine gradations of laryngeal tension necessitated by speech and vocal modulations. Lobulus 4 in the ungulates certainly shows a well marked development and might correspond better with the elongation and greater range of activity of the neck than the lobulus simplex, the most cephalic portion of lobulus C to which has been traditionally allocated the control of the cervical musculature.

From these fragmentary observations, it is clear that it does not seem justifiable to try to draw any definite conclusions as to functional localization in the anterior lobe. The evidence as obtained in this incomplete study does not afford any basis for corroboration or refutation of the diagrammatic localizations which are usually indicated in the various schemas of the cerebellum. It may be possible to arrive at more definite conclusions with the enlargement of the present series.

LOCALIZATION IN THE POSTERIOR LOBE

The case of the posterior lobe, however, is rather different. One of the more striking features noted in this study is the enormous expan-

sion of the parafloccular formation in the aquatic forms. This includes not only *Cetacea* and *Sirenia* but also *Pinnipedia*. *Pinnipedia* show a perfectly definite and characteristic arbor vitae pattern which may be homologized with ease with the other carnivora. The expansion of the arbor vitae of the anterior lobe into the hemisphere follows the arrangement typical for carnivorous animals, and the ansiform formation does not present any significant variations.

Cetacea, however, show a highly distinctive evolution of the arbor vitae which offers many difficulties if analysis and defies dogmatic schematization. The folial pattern also presents many obstacles to the establishment of homologies with the other forms. This applies almost with equal force to both the anterior and the posterior lobes. The parafloccular formations, however, of all the aquatic forms disclose a surprising degree of similarity. Not only is it relatively enormous in all of these forms, occupying from two to three fifths of the entire cerebellar mass, but in its general constitution and organization it presents many striking likenesses. The aquatic forms present the highest degree of axial coördination. This is occasioned, of course, by their aquatic habitat. Their entire existence is passed in an aqueous environment, and to this they have adapted themselves by the acquisition of a type of locomotion which exhibits the most perfect segmental coördination developed by any of the mammalia and can be rivaled only by the progressive movements of the fish and the snake. In addition to this axial coördination of the muscles of the trunk, there is also an extraordinary degree of synergy between the axial musculature of the trunk and the appendicular musculature represented by the anterior flippers, the tail and the posterior extremities, largely incorporated with the tail. These physiologic characteristics seem to be definitely associated with this enormous development of the parafloccular formation, and it would appear highly probable that this type of cerebellar organization is dependent on an aquatic habitat and the necessities imposed on the muscular organization of these forms by their environment. The marked differences in the fore limbs of the sea lion, which are capable of a considerable degree of unilateral independence, from those of the narwhal which have been reduced to mere flippers useful only in progression, is clearly paralleled by the difference in development of the lobulus ansiformis, which in the sea lion and seal is distinctly of the carnivorous type,

whereas in *Cetacea* this part of the cerebellum has lost its clear definition.

It must also be borne in mind that *Pinnipedia*, *Sirenia* and *Cetacea* are highly specialized forms which have a phyletic ancestry quite at variance with the consummation of their adaptive radiation, and their hereditary equipment may represent rudiments either unused or usurped by functional localizations of an unusual character. This may explain the rather extensive development of lobulus 4 in manatee, an animal without a real neck, and lobulus C 2 in *Cetacea*, which have only rudimentary appendicular appendages.

The consideration of the anthropoid series presents indubitable evidence of functional localization in the posterior lobe. One of the most striking results of this study has been the gradual evolution of the form of the arbor vitae and the folial pattern throughout the primate series. Beginning with the marmoset and the lemur, which present a distinctively carnivorous type of cerebellum, the gradual development of the organization of this organ evolves in an orderly series, continuing in *Macacus* and then in *Cynocephalus babuin*, which shows distinct characteristics of the carnivora particularly of lobuli C and B, and is distinctly subordinate to the two types of *Cebidae*, *Cebus lunatus* and *Ateles ater*, both of which are definitely more highly specialized and developed in manual organization than is *Cynocephalus*. The arbor vitae of *Cynocephalus*, if considered independent of its lateral expansion, appears as if it should stand between *Cebidae* and *Simia satyrus*. Even a cursory glance at the folial patterns, however, clearly indicates that *Cebidae* show a more highly differentiated development in the hemispherical constituents of lobulus C, and in particular lobulus C 2. The explanation of these apparently conflicting features offers some difficulties. One, however, may theorize on this point and explain it by the assumption that *Cynocephalus* may show a divergent tendency from the general primate stem toward an increasing manual differentiation which was, however, frustrated by its increasing body bulk which forced it back from an advanced brachiation into a ground living form in which it reverted to a quadrumanal type. Whether this is actually true is difficult to determine. In a rapidly developing series showing in clear detail the gradual evolution of lobulus 4 and lobulus C, which are the characteristic portions of the primate cerebellum, there follow one another *Simia satyrus*, *Gorilla gorilla*, *Anthropopithecus troglodytes* and *Homo sapiens*.

These forms are given in this sequence advisedly from the study of the arbor vitae and of the folial pattern. It seems yet to be a debatable point which of the primate forms is the higher, *Anthropopithecus troglodytes*, the chimpanzee, or *Gorilla gorilla*. The reconstructions of their brain stems and study of microscopic sections present so many conflicting points of view that it is difficult to arrive at any definite conclusion as to the relative position of these two forms in the ascent of man. In many ways the physical organization of the chimpanzee is closer to that of man than that of the gorilla. In his manner of progression, in the comparative freedom of the fore limbs from the necessities of locomotion, in his more delicate bodily structure and in his more tractable disposition, the chimpanzee attains a place more nearly in line with *Homo sapiens* than *Gorilla gorilla*. A consideration of the arbor vitae and of the folial pattern from the point of view of similarity of organization and development to the human cerebellum places *Gorilla gorilla* on a distinctly lower plane than *Anthropopithecus troglodytes*.

The development of lobulus 4 and lobulus C presents a gradual efflorescence from *Simia satyrus* to gorilla, chimpanzee and man. The gradual evolution of lobulus C, and in particular lobulus C 2, without any question, must be associated with the increasing cortical connections of the cerebellum. These pallial contributions reach the cerebellum for the purpose of enriching and perfecting the organization of skilled movements which show such a decided upward trend in *Simia*, gorilla and chimpanzee with its final culmination in man. Confirmation is added to this by the gradual accretions in size of the middle cerebellar peduncle, the great pathway by which the cortex pours its contributions to synergy into the cerebellum. The expansion in lobulus C 2 has taken place pari passu with the enlargement of the cerebral peduncle, the pontile nuclei and the middle cerebellar peduncle. Dr. Cornwall in his specimen of cerebrocerebellar agenesis has been able to follow the fibers of the middle cerebellar peduncle into the pyramidal and suprapyramidal portions of the cerebellum, which would bring them directly into the area under discussion, that is lobulus C 2, and its lateral expansion in what may be recognized as the derivatives of the lobulus ansiformis.

There can be little doubt that this regional aggrandizement is associated with the development of the motor patterns and formulas connected with the acquisition and perfection of skilled movement,

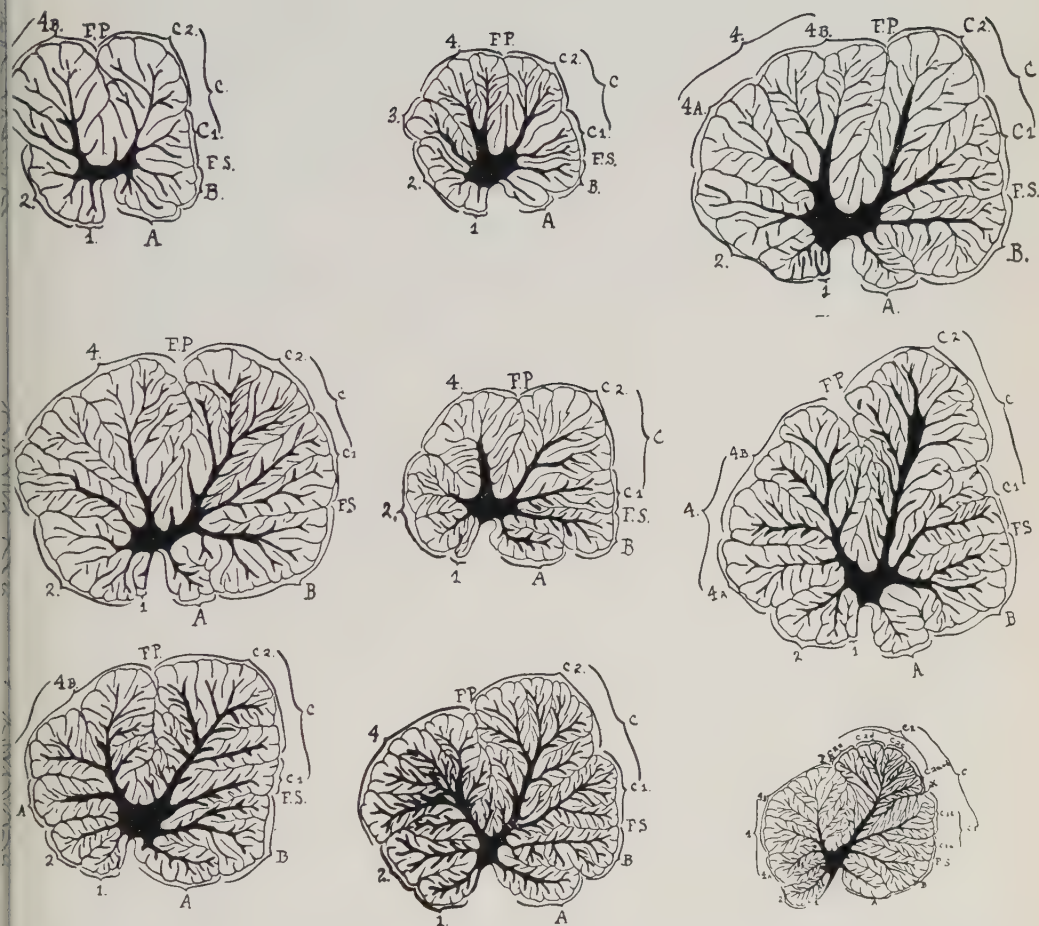


FIG. 40. The arbor vitae of the primates in series shows the gradual evolution which has taken place in this phase of cerebellar organization. The order of precedence does not necessarily indicate the relative positions held by each member of the primate suborder, but does exemplify the advance shown by each successive form in the development of the cerebellum. The points to be emphasized are: (1) the modification in the form of the medullary substance from a transverse bar in the lower forms to the oblique triangular form in man; (2) the development of the lingula; (3) the crystallization of lobulus 4, and (4) the gradual efflorescence and emergence of lobulus C as the dominating feature in the arbor vitae.

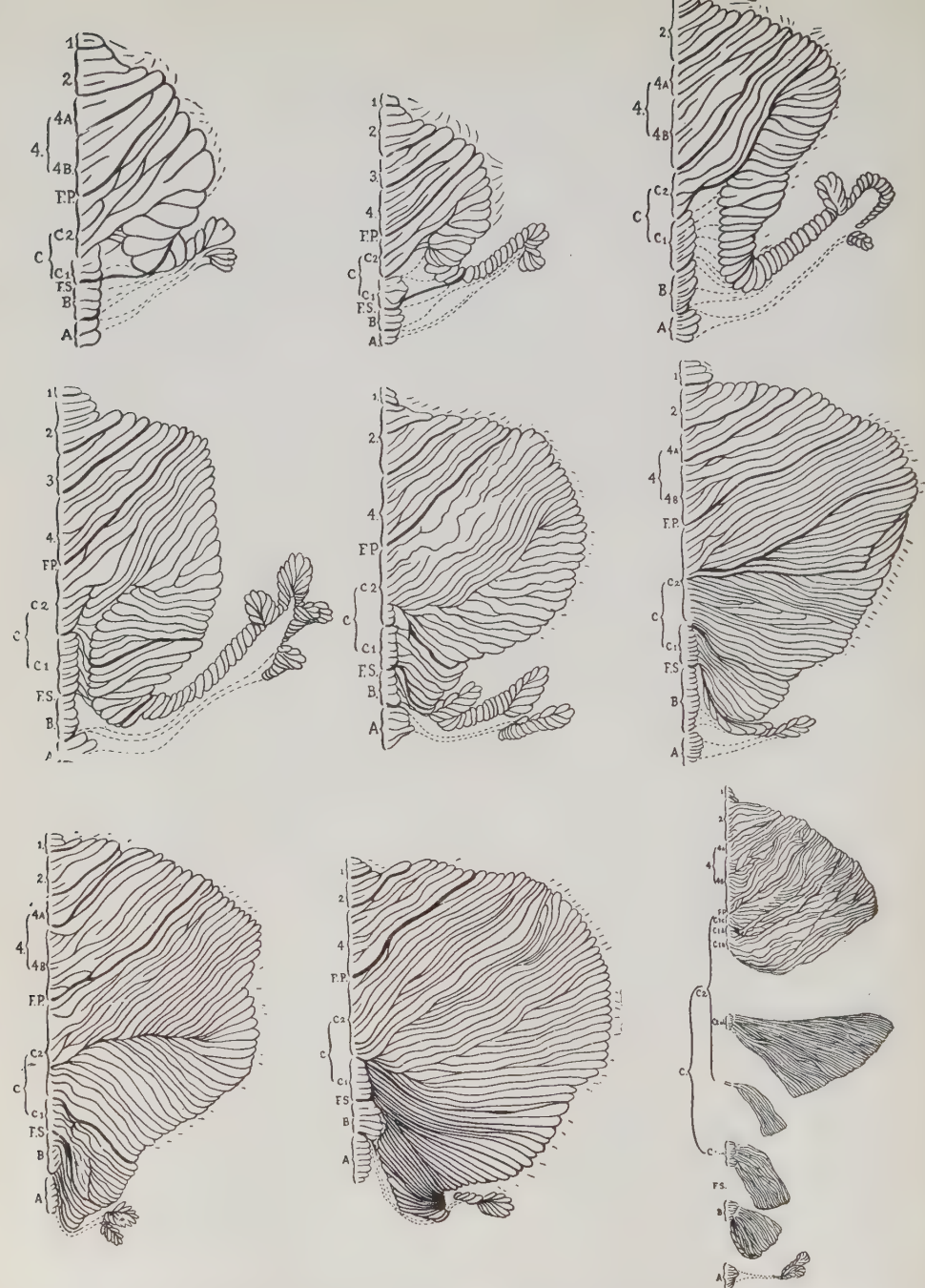


FIG. 41. This series of folial patterns demonstrates the gradual transition through the primate series from *Hapale jacchus* to *Homo sapiens*. The features of general interest which are shown by this comparative representation are: (1) the gradual reduction of the lobulus parafloccularis and its identification with the tonsil; (2) the progressive reduction in importance of the anterior lobe as compared with the posterior lobe; (3) the gradual evolution, and final ascendancy of lobulus C and, in particular, lobulus C 2; (4) the identification of the sulcus horizontalis with the sulcus intercruralis, and (5) the much closer approximation to *Homo sapiens* of *Anthropopithecus troglodytes* than *Gorilla gorilla*.

which reaches its acme in the functional capacities of the upper and lower extremities in their unilateral independence as exemplified by the human hand. One can quarrel but little with the conclusions that this major expansion is probably closely associated with manual differentiation and also with the undeveloped potentialities of the foot. The specialization of the foot has never received the attention which it deserved, for, as Tilney has repeatedly pointed out, the overspecialization of the primates in the development of four hands has steadily handicapped their development, and it is only after the feet have specialized in locomotion that the fore limbs have been freed from the necessities of transportation and attained the opportunity for their complete emancipation.

CONCLUSIONS

1. A modification of Bolk's cerebellar diagram and schema is presented in a division of the anterior lobe into definite vermal and hemispherical portions.

2. The division of the cerebellum into an anterior and a posterior lobe is sufficient, and no useful purpose is served by the addition of a middle lobe.

3. The arbor vitae and folial patterns show that the most cephalic and the most caudal portions of the vermis undergo the least degree of significant modification.

4. The ungulates develop a paravermis in lobulus C and lobulus B.

5. The aquatic forms show a striking uniformity in the development of the lobulus parafloccularis, and this may be associated with the specialization of the axial and appendicular musculature in the particular type of progression necessitated by an aqueous environment.

6. It is perfectly possible to homologize the various subdivisions of the human cerebellum with the accepted constituents of the schematic cerebellar pattern.

7. The sulcus horizontalis magnus appears to be the homologue of the sulcus intercruralis.

8. A definite statement cannot be made from this incomplete study as to functional localization in all of the lobules of the cerebellum.

9. This study offers but little confirmation of the accepted functional capacities of the anterior lobe of the cerebellum.

10. Lobulus 4 and lobulus C, with their associated hemispherical

expansion, show the greatest progressive differentiation and efflorescence. This is definitely associated with the rôle played by the cerebral cortex in its influence over cerebellar unfolding and may be correlated with the perfection of the patterns for skilled movements and the unilateral independence of the fore and hind limbs.

11. Further elaboration of this study may present material of value in further attempts to establish functional localization in the comparative and human cerebellum.

CHAPTER III

THE COMPARATIVE MORPHOLOGY OF THE CEREBELLAR VERMIS, THE CEREBELLAR NUCLEI AND THE VESTIBULAR MASS

EXPERIMENTAL INVESTIGATIONS¹

LOUIS HAUSMAN, M.D.

THE survey of the comparative morphology of the vermis together with the cerebellar nuclei in the various classes of vertebrates, emphasizes not alone the topographical, but as well the structural and functional relation of these parts to the large vestibular component of the middle hindbrain segment.

The question, whether the cerebellum is to be regarded as an organ of bilateral origin or a midline outgrowth in the roof of the fourth ventricle, is quite pertinent to our discussion. Ontogeny and phylogeny point strongly to the development from bilateral anlage, *i.e.*, from the octavolateral or primordial vestibular area, in the dorsolateral part of either side of the hindbrain. There is also evidence that in some of the lower forms, in the absence of a cerebellum these areas at one time functioned by themselves. In *Ammocoete*, this primitive segmental arrangement still persists and in *Necturus*, the symmetrical character of cerebellar growth is plainly manifest.

With the expansion of the sensori-motor field of activity and with the corresponding increase in the behavior resources of the animal, the need for rapid correlation and quick responses led to the centralization of the segmental apparatus in the suprasegmental organs, to meet the demands of economic organization. Accordingly, the more complex correlations of balancing and equilibration, both static and dynamic, resulted in the elaboration of the vestibular apparatus, with the ultimate development of the cerebellum.

The first indication of this particular type of physiological and structural specialization, is found in *Cyclostomes*, the lowest of the

¹I wish to express my great indebtedness to Dr. Adolf Meyer and to Dr. Tilney, for their kindness in putting at my disposal the material which forms the basis of this study.

true vertebrates (fig. 42). In this order, the cerebellum represents only a slightly higher differentiation of its segmental foundation, being hardly more than a commissure for the octavolateral areas, with which it establishes a morphological and functional unity. In the higher vertebrates this stage of evolution is represented by the fundamental cerebellar arch, which occurs as a constant unit throughout the vertebrate phylum and serves as a basis for further cerebellar expansion. In each instance it spans the roof of the fourth ventricle, with the ends

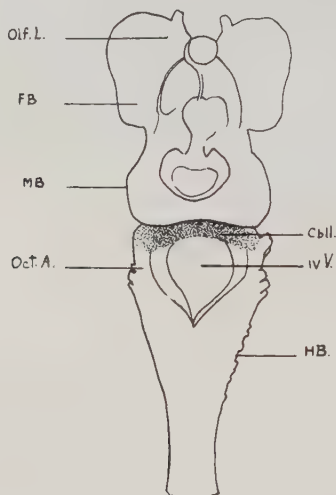


FIG. 42. Dorsal view of the brain of *Petromyzon*. The dotted area represents the extent of the cerebellum (*Cbl.*), which is most primitive in type and equivalent to the fundamental cerebellar arch, connecting the octavolateral areas (*Oct. A.*) of the hindbrain (*HB.*). *Olf. L.*, olfactory lobe; *FB.*, forebrain; *MB.*; *iv V.*, fourth ventricle.

of the arch rooted in the vestibular area of either side. In man it is identified with the inner cerebellar arm or tractus nucleocerebellaris which connects the vestibular mass with the vermis and the roof nucleus (figs. 72 and 73).

The development of the cerebellum indicates its functional relation to the principal organs of balance and equilibrium, its growth in the lower forms reflecting the differentiation of the vestibular and lateral line functions and the influence of the hypothalamus and the optic

lobes. Its expansion in the higher vertebrates is determined by the development of the spinocerebellar and corticopontine systems.

In terms of body growth, this evolution parallels the development of (1) the axial segments, (2) the lateral appendages, (3) the coördination of the body with the limbs and (4) the liberation of the extremities and their independent use for purposes other than locomotion.

The lateral line influence which is most marked in the cyclostomes, fishes and tailed amphibia, is mediated through a series of highly specialized receptors, exceedingly sensitive to pressure changes in the water and to vibrations from neighboring objects. Together with the semicircular canals which in their rudimentary state may be regarded as a specialized portion of the lateral line system, the latter provides the animal with a very fine equilibratory mechanism. In some fishes, this primitive relationship of the labyrinth is retained in the connection of the ductus endolymphaticus with the surrounding water. The most elementary semicircular canals occur in the cyclostomes; Myxinoids having only one canal with a *saccus communis* and *Petromyzon* two canals, an anterior and a posterior, the horizontal being absent.

With the acquisition of these new mechanisms, the cerebellum develops, making its first appearance in the cyclostomes. In the invertebrate phylum it is doubtful, whether a similar representation exists, although according to Edinger—"experiments upon the supraesophageal ganglion in arthropoda indicate that it fulfills functions equivalent or similar to those of the cerebellum in higher animals."

PETROMYZON

The rudimentary character of the cerebellum in *Petromyzon* or Lamprey, is in keeping with the primitive bodily development of the animal; in the larval form, *Ammocoete*, which spends three to four years of its brief existence in the mud, the absence of a cerebellum is more or less in keeping with the life history of the organism which in some respects represents a stage of evolution "intermediate between *Amphioxus* and a very primitive *Craniate*." But in the adult form (*Petromyzon*) which has undergone metamorphosis, one would expect a more highly developed cerebellum, in view of the greater expansion of the sensori-motor field and the increased activity of the animal; for the blind *Ammocoete* in its transition to the anadromous *Petromy-*

zon, gives way to an animal not only capable of ascending the rivers to spawn, but also of depositing its eggs in furrows which it excavates at the river-bottom, before returning to sea. Here we have activity, complex coördinations, quick reactions, yet a cerebellum so primitive that its existence for a time was questioned by some observers. Correlation with the body pattern is much simpler, for the morphological development is very primitive; there are no paired limbs, only an anterior and a posterior dorsal fin in the midline, which is continuous with the caudal structure fringing the protocercal tail, so that locomotion depends on the inter- and intrasegmental activity of the body and tail. It is therefore not surprising that considerable doubt exists concerning the presence of a spinocerebellar system in *Petromyzon*.

To what extent the archaic nature of the cerebellum in this form represents a truly primitive structure or one that has been shaped by degeneration is difficult to determine. However, there is no doubt that it is essentially a lateralis-vestibular organ, only slightly differentiated from its segmental foundation, *i.e.*, the octavolateral area.

In the adult Lamprey, the octavolateral area constitutes a special group of cells in the dorsolateral part of the hindbrain (fig. 42), which receives fibers from the semicircular canals and the lateral line organs, the latter exerting a marked influence on the cerebellar development. It is made up of two parts: an inner vestibular mass and outer structure, the cerebellar crest. The latter is in close relation to the nuclei of the lateral nerves and is absent in vertebrates with no lateral line organs. It is from the inner or primordial vestibular mass, that the cerebellar and vestibular nuclei are ultimately evolved.

The cerebellum in *Petromyzon* exists as a thin ridge in the roof of the fourth ventricle, adjacent to the optic lobes (fig. 42). In this stage, it constitutes the fundamental cerebellar arch and consists of two layers: (1) an inner or caudal layer and (2) an outer or frontal layer.

The inner layer which is cellular, and equivalent to the granular layer of the higher vertebrates, represents a fusion of the two main vestibular nuclei; this is borne out by the striking resemblance of the cellular elements of these parts. Scattered throughout the layer are large cells with well developed dendritic processes in the molecular zone; these are poorly differentiated Purkinje cells in the stage of transition from the cells of the vestibular area to the future granule and true Purkinje cells (Schafer, Johnston, Schilling).

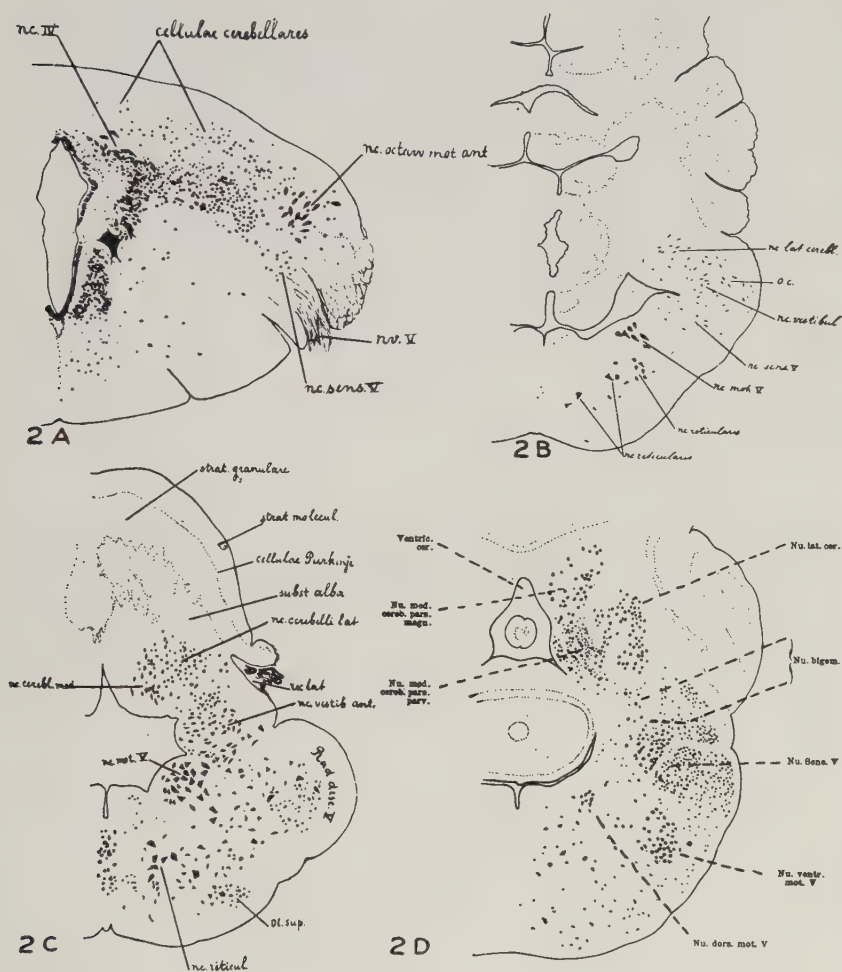


FIG. 43. Cerebellar and vestibular nuclei

A, Transverse section of brain of *Petromyzon fluviatilis*, at the level of the trigeminal nucleus (Van Hoeverll). Cell groups of the cerebellum and the octavolateral area.

B, Section through the hindbrain of *Selache maxima*, at the level of the trigeminal nucleus (Van Hoeverll).

C, Section through the cerebellum of *Alligator sklerops*, at the level of the cerebellar nuclei which are distinct and divided into two groups, a mesial group of darker cells (*nuc. cerebelli medialis*) and a lateral group continuous with the vestibular (*nc. vestib. ant.*) (Van Hoeverll).

D, Section through the cerebellar nuclei of a parrot (*Palaeornis torquata*) (Van Hoeverll).

The outer or fibrous layer is equivalent to the molecular layer of higher vertebrates; it is hardly more than a commissure in *Petromyzon*, and represents a continuation of the fine fibers of the cerebellar crests.

The histological resemblance between the cerebellum and the octavolateral area is further emphasized by the distribution of the eighth nerve to these parts. In addition to fibers from the lateralis-vestibular system, the cerebellum also receives fibers from the optic lobes of the midbrain, from the hypothalamus, from the trigeminal complex and a small bundle (*tractus lobo-cerebellaris*) from the inferior lobes. The important part played by the vestibular mass in the origin of the cerebellum is also reflected in the development of the cerebellar nuclei.

In the dorsolateral part of the hindbrain at the level of the trigeminal nerve is a group of cells, described by Van Hoeverell as the nucleus octavomotorius anterior (fig. 43, A). It consists of large spindle-shaped cells, which send their axons to the tegmentum of the midbrain where they decussate below the level of the oculomotor nuclei, some giving off collaterals to this region on the same side. This is the cerebello-tegmental tract and appears to follow the course of the superior cerebellar arm or brachium conjunctivum in higher vertebrates. Kappers regards this nucleus, as the homologue of the frontal portion of Deiters' or Bechterew's nucleus in the higher animals. Van Hoeverell concurs in this view and states that "in reptiles one still finds the nucleus Deiters grouped into two portions, each of which for a great part gives origin, the one to a tractus Deiters ascendens, the other to a tractus Deiters descendens. In this respect they show much similarity with the separated nucleus octavo-motorius anterior and posterior (Kappers). In some of the lower mammals (Marsupials) something of this separation is still visible."

It would appear then that Deiters' nucleus or certainly the vestibular mass takes part in the formation of the superior cerebellar arm in the lower vertebrates. This is in accord with the conclusions that Bechterew reached in his studies on the myelinization of the brachium conjunctivum, in which he was able to distinguish four distinct bundles. He found that in a human foetus 28 cm. long, the most ventral part of the brachium conjunctivum, which is the first to become medullated, forms a commissure between the vestibular nuclei and is in no connection with the cerebellum.

Mesial to the nucleus octavomotorius anterior, is another group of

smaller cells, designated "cellulae cerebellaris" by Van Hoesell (fig. 43, A). The axons of these cells also take part in the formation of the cerebello-tegmental tract, which Schilling considers homologous with the brachium conjunctivum. This nucleus appears to be the forerunner of the vermis nuclei in higher vertebrates. If this is so, then Bechterew's findings are in further agreement, for he noted that in human foetuses about 33 cm. long, the most dorsal part of the brachium conjunctivum, which is medullated next, appears to be connected with the nucleus fastigii; the fibers decussate and pass to the red nucleus.

FISHES

The dictum of Haeckel concerning cyclostomes, that "they are further removed from fishes than fishes from man" is nowhere better exemplified than in the wide divergence of their cerebellar patterns.

The cerebellum of fishes presents a distinct departure from all other types in the peculiar character of its expansion. If we take into account the numerous ways in which these powerful swimmers are adapted to the particular medium in which they live, this is not at all surprising. Balancing in water is a performance that requires an exquisitely sensitive equilibratory mechanism. Curiously enough, it is in those vertebrates adapted to flying and to swimming and in whom the patterns of locomotion are so complex and varied that the cerebellum first shows a definite advance and distinct departure from the preceding forms.

In the fishes, the equilibratory capacity, both static and dynamic, is enhanced by the acquisition of a third semicircular canal and two sets of paired lateral fins, (in addition to the median fins) to reinforce the lateral line and labyrinthine systems.

The lateral fins, contrary to the usual belief, are used more for balancing and guiding the body, than for propulsion, which is chiefly the function of the powerful muscular tail. Were it not for the action of the paired pectoral and pelvic fins, which represent the fore- and hindlimbs respectively, the fish would float belly upwards, due to the dorsal position of the center of gravity. The anal and dorsal fins, act as a median keel, which serves to steady the swimming and when removed causes the animal to wobble. The lateral fins on the other hand, act as lateral keels and when removed on one side cause the fish to roll over to that side.

The pectoral fins are rarely absent and vary greatly in form and size in the different fishes, being exceptionally large in Elasmobranchs; in the latter the tail, however, is poorly developed and probably useless as a locomotor organ.

The action of the tail in propelling the fish, resembles that of the stern-oar used in sculling a boat. The motion of the tail throws the body of the fish into never less than two curves, which occur always

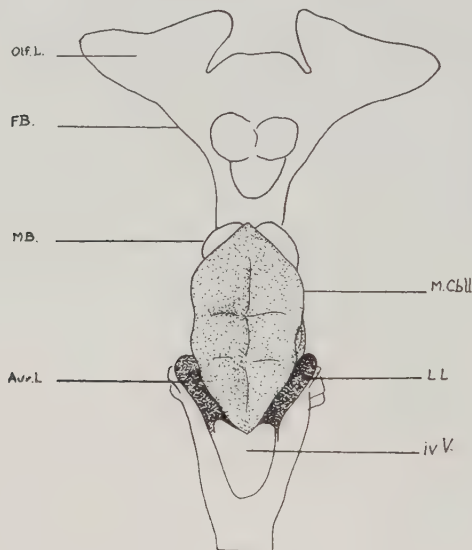


FIG. 44. Dorsal view of the brain of *Scyllium canicula*. The dotted area represents the cerebellum. *M.cbll.*, the median body of the cerebellum; *L.L.*, the lower lip or fundamental arch of the cerebellum; *Aur.L.*, auricular lobe; *Olf.L.*, olfactory lobe; *FB.*, forebrain; *Mb.*, midbrain; *iv V.*, fourth ventricle.

in pairs and are complementary to one another. The effort of locomotion is minimized by an air-bladder, which renders the fish, bulk for bulk, of the same weight as the water. In a large number of fresh water Teleosts, the acoustic organ is in more or less intimate connection with the air-bladder—an arrangement calculated to register the variations in hydrostatic pressure.

In view of these extensive provisions for equilibration, it is not surprising to find in fishes a striking advance in the cerebellar pattern

and organization (figs. 44 and 45). Three distinct types are recognized: the cerebella of Elasmobranchs, Ganoids and Teleosts present a wide range of form and pattern (figs. 46, 47, 48, 49). However, in all three, the fundamental arch remains quite constant in its relation to the octavolateral area. In Elasmobranchs, this structure as it curves around the lateral recess, gives rise to a lateral prolongation, the auricular lobe (figs. 44 and 45) the forerunner of the flocculus in

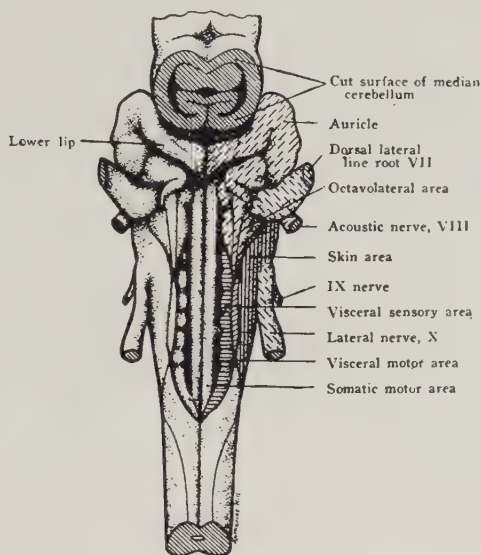


FIG. 45. The medulla oblongata of *Squalus acanthias* seen from above after removal of the membranous roof of the fourth ventricle. The posterior part of the dorsal median body of the cerebellum has been cut away to expose the lower lip (Herrick).

the higher vertebrates. It is through a fusion of the upper ends of this lobe that the arch is formed; in figures 44 and 45 it is indicated as the lower lip in the roof of the fourth ventricle. Grossly, it resembles a similar structure in cyclostomes, but functionally it evinces further specialization, in keeping with the greater differentiation of the scattered Purkinje cells. Whereas in cyclostomes (and in amphibia) the arch receives all the cerebellar tracts, in Elasmobranchs there is a separation of the lateralis-vestibular from the nonvestibular system;

the former going to the arch alone, the latter to a new structure—the large unpaired dorsomedian evagination (figs. 44, 45, and 46) which

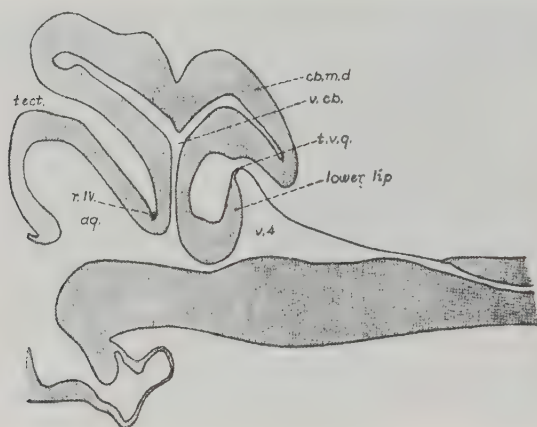


FIG. 46. Median section of the cerebellum of *Acanthias*. Type Elasmobranch. *Tect.*, tectum mesencephali; *aq.*, aqueduct of Sylvius; *r. iv.*, root of fourth nerve; *v.cb.*, cerebellar ventricle; *cb.m.d.*, dorsal median body of cerebellum; *t.v.g.*, tenia of fourth ventricle; *v.4*, fourth ventricle (Van der Horst—Herrick).

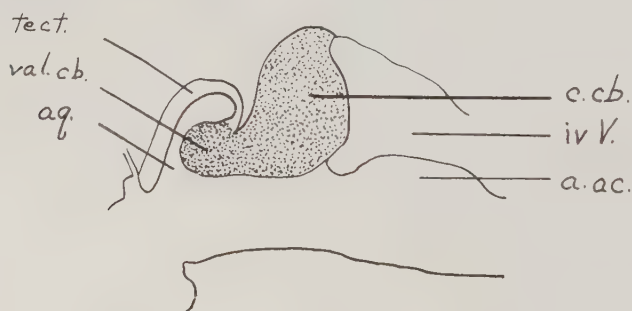


FIG. 47. Diagram of the cerebellum of the sturgeon, *Acipenser*, in parasagittal section. Type Ganoid. The dotted area represents the cerebellum. *C.cb.*, corpus cerebelli; *val.cb.*, valvula cerebelli; *a.ac.*, octavolateral area. Modified from Herrick.

is superimposed on the arch. Its growth is probably determined by the acquisition of the lateral appendages and by the increased size of

the body and the concomitant development of the spinocerebellar tracts. It receives fibers also from the inferior olives, the midbrain and the hypothalamus.

The results of removal of this dorsomedian evagination in Elasmobranchs indicate that it is functionally independent of the vestibular apparatus (Tilney). At no time do the animals manifest any inability to maintain their optimum posture, which is the case when the semicircular canals or vestibular parts are injured. It appears to be concerned with the regulation of inherent automatic associated

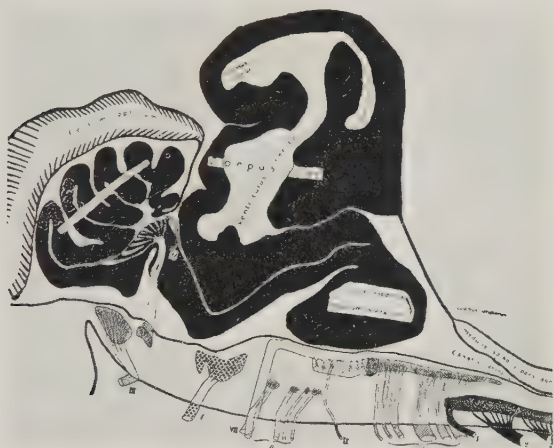


FIG. 48. Median section of the cerebellum (in black) of *Megalops cyprinoides*. Type Teleost. Note the marked development of the valvula (van der Horst).

movements; especially with the synergetic action of the muscles of the body, tail and lateral appendages.

The cerebellar nuclei in Elasmobranchs also give evidence of further differentiation, especially with regard to their dorsal shifting. The nucleus lateralis cerebelli, described by Van Hoeverll, Kappers and others, is on cross-section continuous dorsally with the substance of the cerebellum and ventrally with the tegmentum of the hindbrain (fig 43, B), particularly with the cells of the vestibular mass. Adjacent to this cerebellar nucleus, is a small group of cells (marked o.c. in figure 43, B), which have a different axial position. Van Hoeverll looks upon these as a ventral continuation of the main cerebellar nucleus.

According to the latter, the nucleus cerebelli receives fibers from the cerebellar cortex and from the vestibular and lateral line systems; it gives off fibers ventrally to the midbrain and bulb, resembling in this respect the cerebellar nuclei of higher vertebrates. The fibers to the midbrain decussate there at the raphe, to be lost in the region of the oculomotor nuclei; they are probably homologous with the superior cerebellar arm of mammals, although an exact identification cannot be established due to the fact that the red nucleus is not well defined in sharks (DeLange).

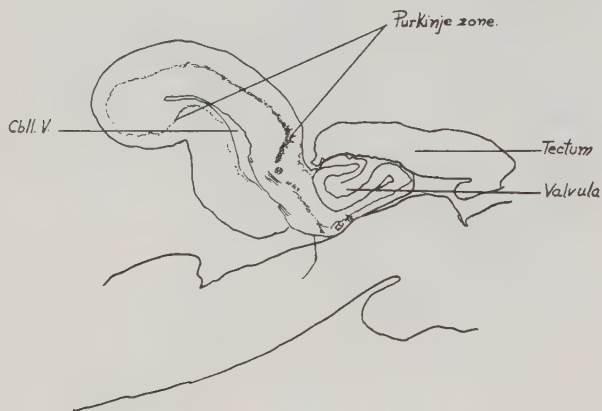


FIG. 49. Median section of the cerebellum of a pike. *Cbl. V.*, cerebellar ventricle.

In contrast to the Elasmobranchs, the Ganoids present a cerebellum which is less expansive. The dorsal evagination gives way to a ventral invagination or valvula, which in some forms almost fills the midbrain ventricle and may be looked upon as a cephalic prolongation of the fundamental arch, connected chiefly with the lateral line system (fig. 47).

The Teleostean cerebellum (figs. 48 and 49) which is a composite of the Elasmobranch and Ganoid types, is much more inclusive than either of these forms, containing as it does both the evaginated dorsal median body and the invaginated valvula in addition to the other structures that have thus far been identified; yet, withal it is compact. The dorsal median body in its connections and functions, resembles that of Elasmobranchs.

The cerebellum of Teleosts is subject to great variation in the different species, not only with regard to the fiber systems (as Addison pointed out), but also with regard to the size of the valvula and the cerebellar crests, both of which represent extensions of the vestibulo-lateralis systems. It is pertinent to note here, that in some forms, the crests fuse above the fourth ventricle to form the "conrescence" of the lateral lobes, which functions with the octavolateral area (fig. 48). The "pars postrema" and the "eminencia granularis" also belong to the vestibulo-lateralis system.

The valvula in its relations to the lateral line centers of the hind-brain and midbrain, from the latter of which it receives the tractus mesencephalicus posterior, resembles the primitive cerebellar plate of *Petromyzon*. This has been substantiated by the findings of Addison, van der Horst and Kappers. Ingvar has pointed out that the distribution of the lateral line and vestibular fibers offers a means of determining the oldest parts of the cerebellum; in his study of the distribution of the vestibular nerve by means of degeneration experiments, he employed this method as a criterion for determining the oldest parts of the mammalian cerebellum.

From a careful analysis of the development of the cerebellum in the different fishes, it is evident that the diversity of pattern is closely related to the distribution of the various fiber systems, forecasting the principle of functional localization manifested in mammals. The vestibulolateralis field including the arch with its prolongations (valvula and auricles), is to be differentiated from the spinocerebellar field, *i.e.*, the dorsal median body, with its optic and somesthetic components. It is difficult to homologize the dorsal evagination with any structure in the higher vertebrates, although there is some resemblance to the cerebellum of the alligator.

AMPHIBIA

The cerebellum of Amphibia marks the transition from aquatic to terrestrial life. The study of this species reveals marked differences, which are peculiar to the habitat of the animal and reflect the extent of its adaptation to marshes and to land.

In contrast to fishes, the cerebellum of amphibia is very rudimentary and resembles the primitive organ of the cyclostomes (fig. 50). There are two types, belonging to (1) urodela (salamander, *necturus*,

etc.) with well developed tail and lateral line organs and (2) anura (frog).

The development of the cerebellum in urodela in many respects recalls the larval form of *Petromyzon* (Ammocoete). According to Herrick, who has contributed so richly to our knowledge of this species, "in the simpler types, there is no cerebellar tissue developed in the middorsal plane . . . with the exception of some commis-

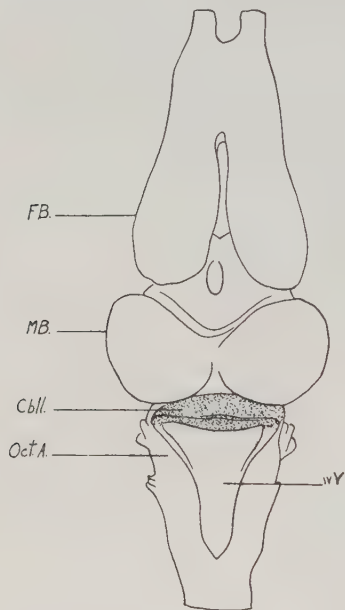


FIG. 50. Dorsal view of brain of frog (*Rana esculanta*). The dotted area represents the cerebellum (*cbl.*). *FB*, forebrain; *MB*, midbrain; *OctA*, octavolateral area; *ivV*, fourth ventricle.

sural decussating fibers." The latter are to be differentiated from the "corpus cerebelli" formed on either side by a thickening in the cephalic part of the octavolateral area (fig. 51).

In adult necturus, Herrick has described an eminence in the floor of the fourth ventricle (fig. 51) caudal to the corpus cerebelli, which projects into the lateral recess and contains the nucleus cerebelli; the latter is made up of large cells whose axons form the cerebellotegmental tract, similar to that described in *Petromyzon*.

The development of the cerebellum in the frog closely follows that of neoturus and brings to light definite changes, which are undoubtedly determined by the transition to terrestrial life.

The differences between the cerebellar patterns of anura and urodela, are in part due to the disappearance or the lateral line system in the former at metamorphosis. The lateral line and vestibular systems which are both present in the larval stages, undergo changes

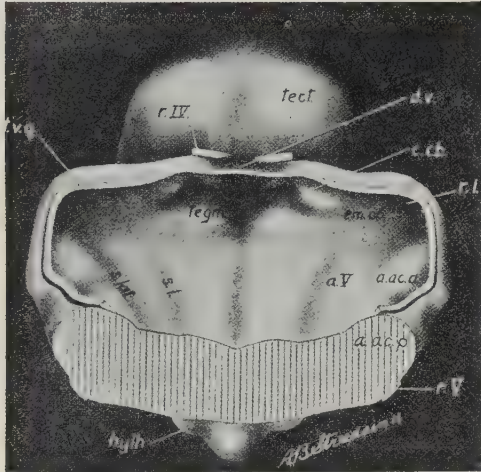


FIG. 51. A wax model of the cerebellar region of a 20-mm. larva of *Amblystoma tigrinum*. The specimen is seen from behind and slightly from above so as to look under the overarching body of the cerebellum into the lateral recess. By reason of the angle from which the model is viewed the fourth ventricle appears greatly foreshortened in the cephalocaudal direction. *d.v.*, decussatio veli; *C.cb.*, corpus cerebelli; *r.l.*, lateral recess; *em.cb.v.*, ventral cerebellar eminence (nucleus cerebelli); *a.v.*, area trigemini; *a.a.c.a.*, octavolateral area, anterior lobe; *a.a.c.p.*, octavolateral area, posterior lobe (Herrick).

in the matured form so that the lateral line system drops out and only the vestibular remains. As a result, the auricular lobe, which in urodela receives lateral line, vestibular and trigeminal fibers, is not as well developed in the frog.

The change from an aquatic existence is further evidenced by the greater development of the spinocerebellar system; this is in keeping with the growth of the strong legs, which are so essential to the frog's

singular type of saltatory bipedism. In consequence, the corpus cerebelli increases in size and by reason of its fusion with the ventral cerebellar eminence produces an organ which is more massive than in cyclostomes or urodela.

A sagittal section in the midline (fig. 52) reveals the cerebellum as a tongue-line projection in the roof of the fourth ventricle, immediately caudal to the tectum. Histologically, the three layers characteristic of the mammalian cerebellum are clearly differentiated; a well defined Purkinje zone separates the molecular and the granular layers. According to Larsell, "all the elements characteristic of the mammalian cortex except basket cells, Golgi cells, and the superficial

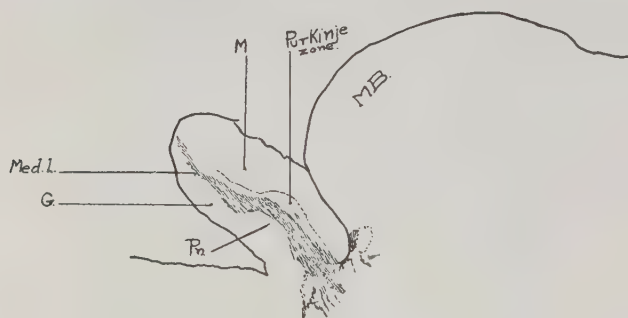


FIG. 52. Median section of cerebellum of frog. *M*, molecular layer; *G*, granular layer; *Pn.*, projection of granular layer into medullary layer (*Med.L.*), *MB.*, midbrain.

stellate cells, have been found, but in less specialized form than in mammals."

Of special interest is the Purkinje layer, which is quite broad, being from two to four cells deep. The cells, although they are not characteristically pyriform are well differentiated and in the position and distribution of their dendritic processes closely approximate the mammalian type. The striking feature is an indentation of the medullary zone by the granular layer (fig. 52), which is most marked near the midline and gradually thins out laterally. It is very marked in reptiles and was first called to my attention by Adolf Meyer in the study of the cerebellum of *Uromastix*, a Syrian lizard.

If we regard this structure as the forerunner of the primary cerebellar fissure, which its position strongly suggests, then the cerebellum

of the frog may be said to present the homologues of the anterior and posterior lobes of the mammalian vermis.

The cerebellum of the frog, like that of the cyclostomes, fishes and higher vertebrates, is formed by a fusion of the rhomboidal lip in connection with the octavolateral area. The ventral cerebellar eminence, contains the nucleus cerebelli which in this order also is directly continuous ventrally with the tegmentum of the hindbrain. Larsell found in Golgi preparations that the nucleus contains "multi-polar cells whose axones pass rostrally and medially, in part, to form the brachium conjunctivum."

This nucleus is to be regarded as the precursor of the roof nucleus and part of the dentate nucleus. In this respect our concept of the dentate nucleus needs revision. The latter in mammals and man may be said to consist of two parts (1) an older part made up of the intermediate nuclei and (2) a more recent acquisition, the dentate nucleus proper, which appears with the development of the cerebellar hemispheres. It is important to recognize that the intermediate nuclei (*globosus* and *emboliformis*) are also part of the dentate mass and constitute its oldest portion. It will become more evident in the higher vertebrates that these nuclei hold the same relation to the principal dentate nucleus, that the phylogenetically older accessory part of the inferior olive holds to the more recently acquired, principal or neolive. For that reason the intermediate nuclei should be designated as accessory dentate or paleodentate to emphasize their primitive character, in contrast to the principal or neodentate nucleus which develops with the cerebellar hemispheres and therefore appears for the first time in mammals.

Accordingly, the nucleus cerebelli in Amphibia and possibly in lower forms may be considered the forerunner of the roof and paleodentate nuclei of the higher vertebrates, although not yet incorporated within the cerebellum.

Experiments

In experiments on the frog, an attempt was made to determine the effects of lesions of the cerebellum and vestibular area. In this animal the problem is greatly simplified; the experimental technique is not complicated and the parts in question are readily exposed, without damage to the surrounding tissue; in addition, the effects of shock are greatly diminished.

An incision in the left octavolateral area alters the animals posture at once. The frog lies on its belly in a sprawling reptilian attitude, but only for a few moments, for it is soon able to sit up at a good angle, with the forelimbs partly extended and the hindlimbs flexed, the left less so than the right. However, in comparison with the normal frog, the sitting angle is not as great. In this sitting position, it inclines toward the left side, the left fore- and hind limbs being bent slightly under the body. There is no paralysis and the animal circles to the side of the lesion. In going forward, the frog seldom leaps but crawls, and sometimes circles clumsily to the right, dragging the extremities of the left side. This is also brought out when the animal is put on its back; it rights itself invariably by turning over on the right side, no matter how much it is tilted towards the left. When touched the frog is able to leap but not far.

Some what similar disturbances, but more intense, are produced by cutting the cerebellum itself. The animal at once loses its optimum posture, being able, however, to sit up by the second day. But it cannot leap; it goes forward clumsily and quickly on its belly, with coördination markedly impaired. The pattern of motility is one of disintegrated ataxic crawling with a marked tendency to fall to one side. There is a very evident lack of coördination between the body and extremities. When touched the animal circles around and around in one direction, with the caudal end of the body more or less fixed and serving as a pivot.

When put on its back, the animal does not turn over, nor does it make any attempt to right itself, no matter how much it is stimulated.

The same exposure, without however cutting any part of the cerebellum, produces no change in the animal's activity or posture.

From these experiments, it is evident that the cerebellum and the octavolateral area of the frog have vestibular functions in common; lesions of these parts produce changes characteristic of injury to the semicircular canals. In addition, the cerebellum itself has other functions, similar to those ascribed to the dorsal median body of elasmobranchs, *i.e.*, for the synergetic action of the muscles of the trunk and limbs.

REPTILES

In reptiles, the coördination of the body with the extremities assumes a very important part in determining the cerebellar type.

At first glance, the reptilian cerebellum appears to be not much higher than the primitive type seen in *Petromyzon*. However, on closer

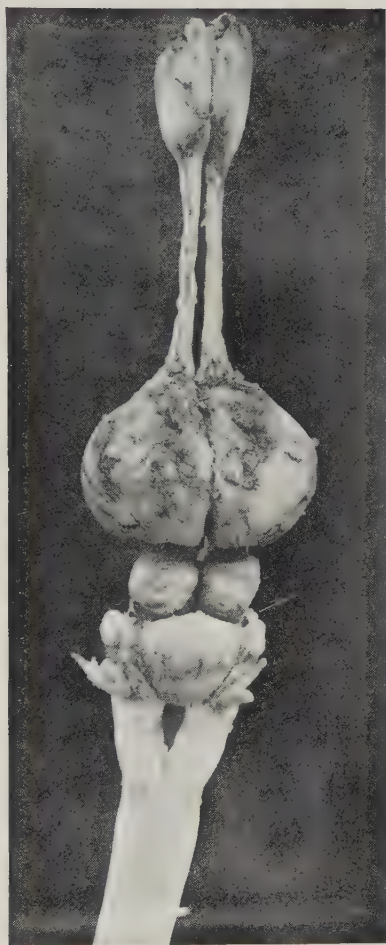


FIG. 53. Dorsal view of brain of alligator (from the collection of Adolf Meyer)

inspection, definite changes of a progressive character can be observed: the body of the cerebellum is considerably enlarged (fig. 53) corresponding to the increase in the size of the spinocerebellar tracts; in

addition, the first signs of cerebellar lobulation make their appearance.

In the different classes of reptiles (as in the fishes) there are wide variations of cerebellar pattern depending on the particular type of locomotion and on the extent to which the body and extremities are used for that purpose. Three distinct types are recognized: the snake, the lizard and the alligator.

The smallest and simplest type of reptilian cerebellum occurs in the snake. It is represented by a thick elongated plate in the midline (fig. 54) (*pars interposita* of Larsell), tapering markedly at its caudal

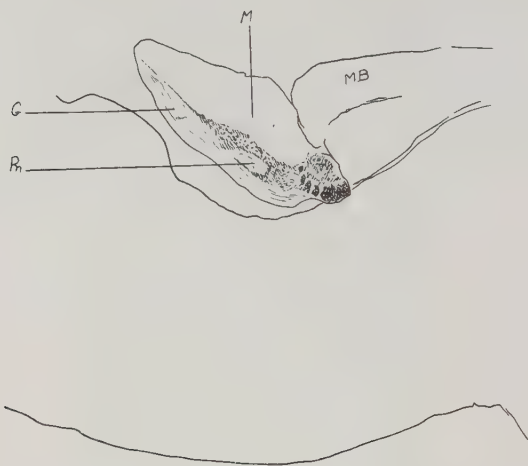


FIG. 54. Median section of cerebellum of snake. Note the projection (*Pn*) of the granular layer into the medullary layer.

tip; the auricular lobes and lateral parts are present, but very poorly developed.

Special significance attaches to this type in view of the absence of extremities, which offers an excellent opportunity for studying the intersegmental body movements in pure culture. It is of interest to note that the cerebellum of the snake grossly resembles that of *Petro-myzon*, another animal without lateral appendages. Histologically, however, the molecular, granular and Purkinje layers are well differentiated. The latter presents the same indentation noted in the frog (fig. 54). It was observed in several different series of sagittal sections, being always most marked in and near the midline, and

thinning out laterally. It occurs at the juncton of the middle and anterior thirds, at which point the cerebellum is thickest.

From the cerebellum of the snake to that of the lizard *Varanus*, a distinct advance takes place, although intervening forms are not without interest.

The simplest types of lizard cerebellum is seen in *Anniella nigra*, a legless lizard, which burrows in the sand; in the size of its cerebellum it also resembles the primitive type of *Petromyzon*.

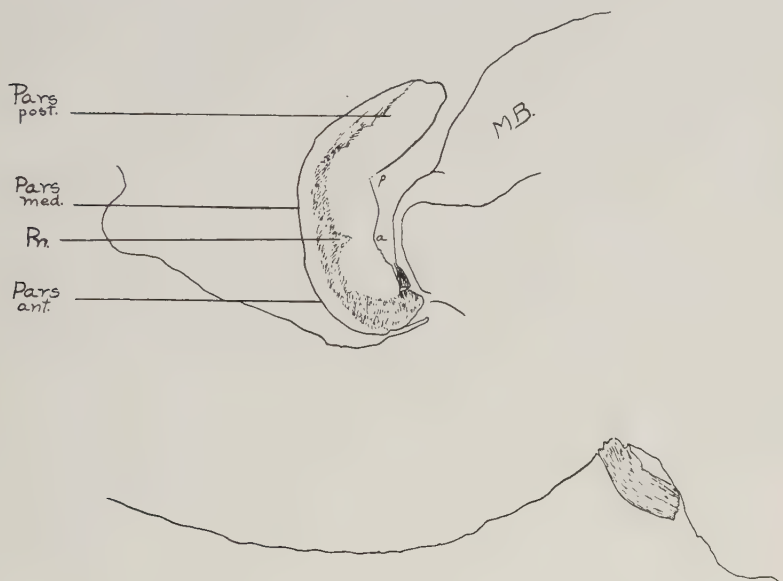


FIG. 55. Median section of cerebellum of lizard. The projection (*Pn*) of the granular layer has broken through the medullary layer into the molecular. Note the two transverse incisions "a" and "p" on the cephalic surface.

The characteristic type of lizard cerebellum occurs in *Varanus* (fig. 55). In this species, the cerebellum takes on a new form and gives evidence of fissure-formation, emphasizing the transverse axis of the organ. A new and definite variation is noted in the peculiar eversion of the cerebellar plate, so that the free tip is reflected cephalad, in proximity with the tectum of the midbrain. As a result, the granular layer instead of being internal is external, and the molecular layer internal. In other words the condition in lower and higher vertebrates is reversed.

The inner or cephalad surface of the cerebellum is marked by two transverse incisures, which divide the organ into three more or less equal parts (fig. 55). At the level of the lower incisure, the Purkinje layer is pierced by a mass of cells, identical with those of the granular

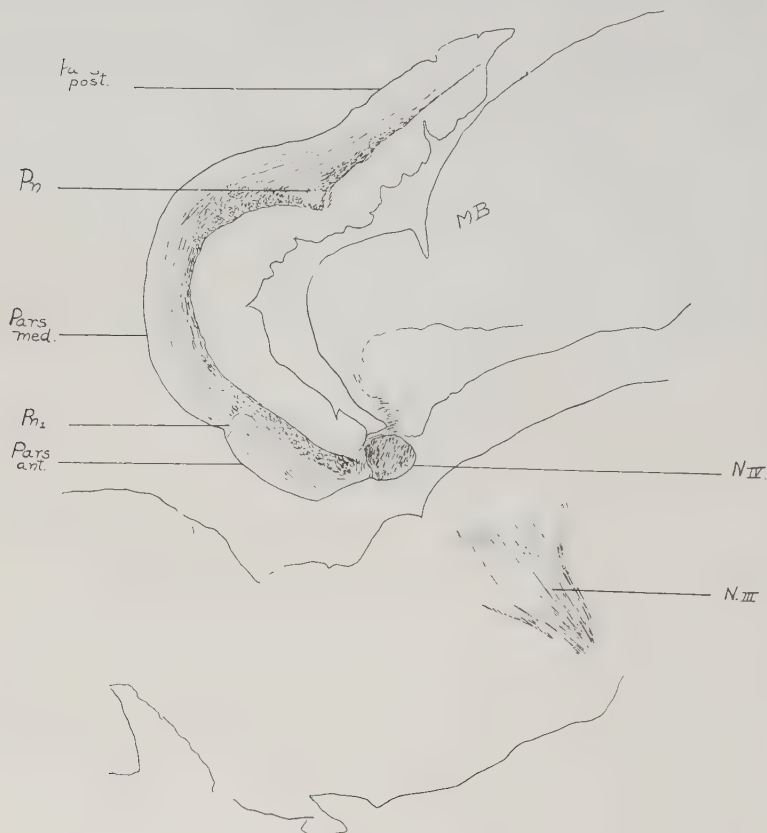


FIG. 56. Median section of cerebellum of Iguana.

layer. This corresponds to the projection described in the cerebellum of the snake and frog, but in *Varanus* it is much more pronounced, actually invading the molecular region. It was identified and studied in several different series of sagittal sections, being most marked mesially.

This type of everted cerebellum, which is so characteristic of the

lizard group, attains its greatest development in *Iguana* and *Uromastix* (figs. 56 and 57).

In the latter, the eversion is so great that the free cephalic end of the cerebellum is almost at right angles to the basal portion and rests directly on the roof of the midbrain. De Lange has pointed out that this unusual type of cerebellar eversion occurs also in the early human

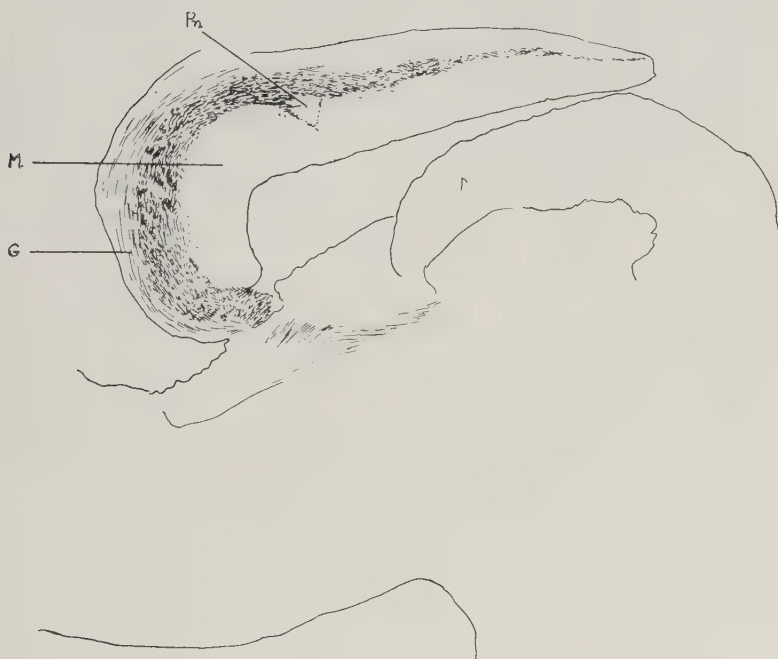


FIG. 57. Median section of cerebellum of *Uromastix*. Note the marked eversion of the cerebellum and the relative positions of the molecular (*M*) and granular (*G*) layers, the projection (*Pn*) is very marked.

fetus. Although the transverse incisures are not very evident in the cerebellum of *Uromastix*, the granular projection, however, is very distinct and breaks through the Purkinje layer to invade the molecular zone (fig. 57). The point of the projection is in relation to a blood vessel in several of the mesial sections.

The cerebellum of *Iguana* typifies the characteristics of the organ in the lizard family. The eversion, the indentation of the Purkinje layer and the transverse fissures are all present. The fissures, how-

ever, instead of appearing on the cephalic surface of the cerebellum, as in *Varanus*, appear on the external or caudal surface and divide the organ into three parts—anterior, middle and posterior (fig. 56).

The granular projection in the Purkinje layer is quite pronounced and has shifted posteriorly. As usual, it is most developed mesially, thinning out laterally. Another incisure (*Y* in fig. 56) was observed at the junction of the middle and anterior parts, appearing however in only a few sections in the midline. Whether it is of any significance is doubtful.

The correlation of this projection with the primitive fissures of the cerebellum presents a difficult problem. In the lizard, its position

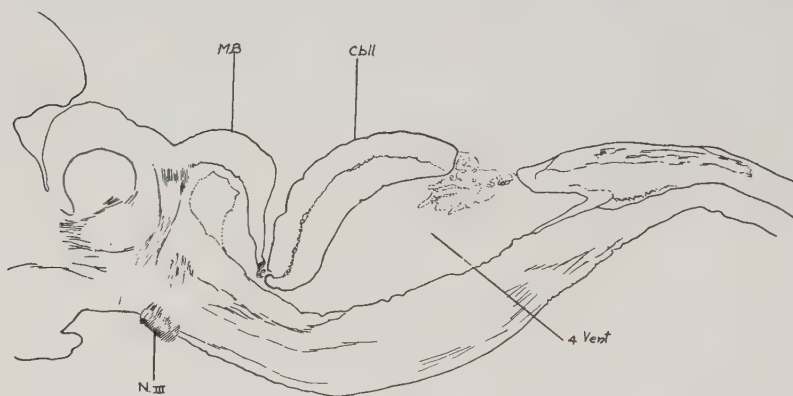


FIG. 58. Median section of brain of turtle. The eversion of the cerebellum in the previous figures 13, 14, 15, is now reversed and approaches the inversion of the cerebellum of the alligator (fig. 59).

and relations suggest the primary cerebellar fissure described by Elliot Smith in mammals. In *Inguana* and *Uromastix*, however, it has shifted posteriorly and suggests rather the prepyramidal sulcus of the higher vertebrates. Respectively, they suggest the sulcus cerebellaris anterior and the sulcus cerebellaris posterior, of the alligator's cerebellum.

In the alligator, which belongs to the order of crocodilia and presents the third and most advanced type of reptilian cerebellum (fig. 53), the process begun in *Varanus* goes on to definite lobulation, so that anterior, middle and posterior lobes are plainly recognized. The cerebellum is quite different in appearance from the reptilian form

thus far described. In contrast to *Inguana*, the eversion of the latter is replaced by inversion, with flexion taking place at the two superficial incisures and producing three distinct parts, which have been identified by Ingvar as lobus anterior, lobus medius and lobus posterior (fig. 59). This stage of cerebellar development corresponds to that of the three months human fetus (DeLange.) In the crocodilia and lizards, the basal or anterior lobe, more or less retains its original position, its longitudinal axis not deviating much therefrom. The

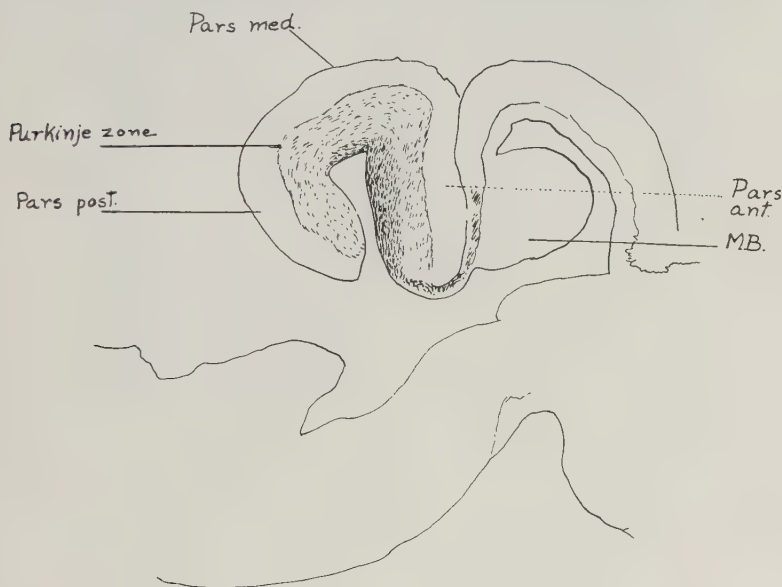


FIG. 59. Median section of brain of alligator. The cerebellar inversion is complete and presents three distinct parts: anterior, middle and posterior.

inversion of the cerebellum that appears in crocodilia, is forecast to a slight extent in the turtle (fig. 58). The latter does not reveal the granular projections noted in the other forms.

In all reptiles, the auricular lobe or flocculus is poorly developed, in comparison with the lower and higher vertebrates; it is scarcely visible in the snake. This is due to the absence of the lateral line system, so prominent in the lower vertebrates; furthermore the vestibular connections are not developed to the same extent as in mammals, as a result of the inferior development of the semicircular canals.

However, between the body of the cerebellum and the auricular lobe on the same side, a new structure develops. This region together with the primitive corpus cerebelli, has been designated by Larsell as the "pars lateralis;" it is probably chiefly concerned with the coördination of leg movements, and appears to be the primitive representa-

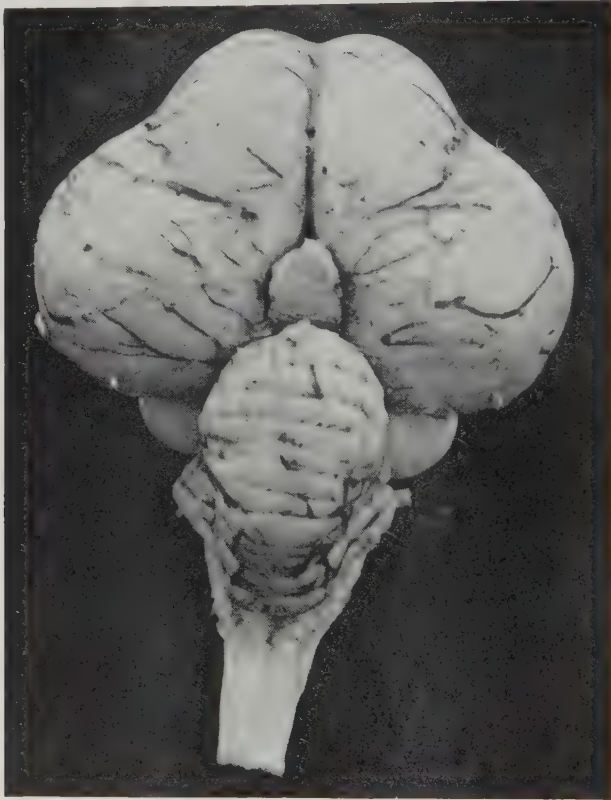


FIG. 60. Dorsal view of brain of ostrich (collection of Adolf Meyer)

tion of the lobus ansiformis, which Bolk has described in mammals and correlated with the paired appendages. It has also been observed by Larsell in the cerebellum of the frog. As to be expected, it is degenerated in the snake, in keeping with the absence of extremities.

On superficial examination, the cerebellum of the alligator (fig. 59)

resembles that of the pike (fig. 49) disregarding the valvula in the latter. However, correlation with the higher vertebrates is somewhat more certain, by reason of the anterior and posterior sulci of the alligators cerebellum which may be homologized with the primary and secondary sulci of mammals, respectively. The posterior cerebellar fissure is deepest mesially, thinning out laterally to the region of the flocculus and resembling in this respect the fissura parafloccularis.

It is evident that in reptiles, the development of the cerebellum shows a distinct advance toward the mammalian type. Histologi-

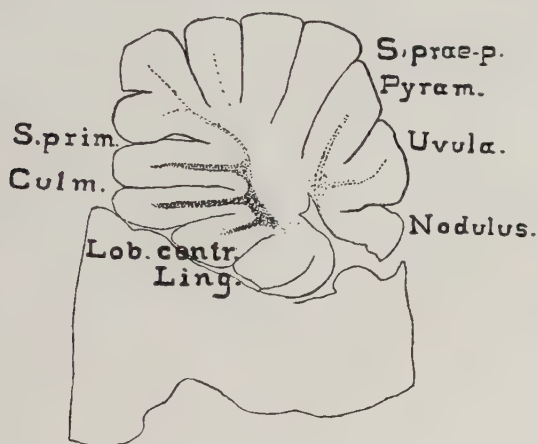


FIG. 61. Median section of cerebellum of a pigeon with the termination of the spinocerebellar tracts. Marchi stain (Ingvar).

cally, this progress is quite marked. Cajal has described real basket cells, which are typical of the higher forms, and do not occur in the cyclostomes, fishes or amphibia. The cerebellar layers are very distinct and the Purkinje cells clearly differentiated.

There is also a distinct advance in the differentiation of the cerebellar nuclei, which have become incorporated within the cerebellum itself (fig. 43, C). The primitive nucleus cerebelli of lower animals, is plainly differentiated in the alligator, into a mesial and lateral part. The continuity with the hindbrain tegmentum, particularly with the vestibular mass, is still retained. In this area, Van Hoeverl, in agreement with Gordon Holmes distinguishes three distinct nuclei:

"the nucleus magnocellularis dorsalis, which contains the greater part of the fibers of Radix posterior; further a nucleus laminaris, which may be regarded as being probably a secondary cochlearis nucleus, and the nucleus ventralis, which certainly is to be regarded as vestibular nucleus." The latter consists of two parts; the large cells forming Deiters nucleus and the small cells the nucleus vestibularis anterior (fig. 43, C). In the alligator, these two cell-types merge into one.

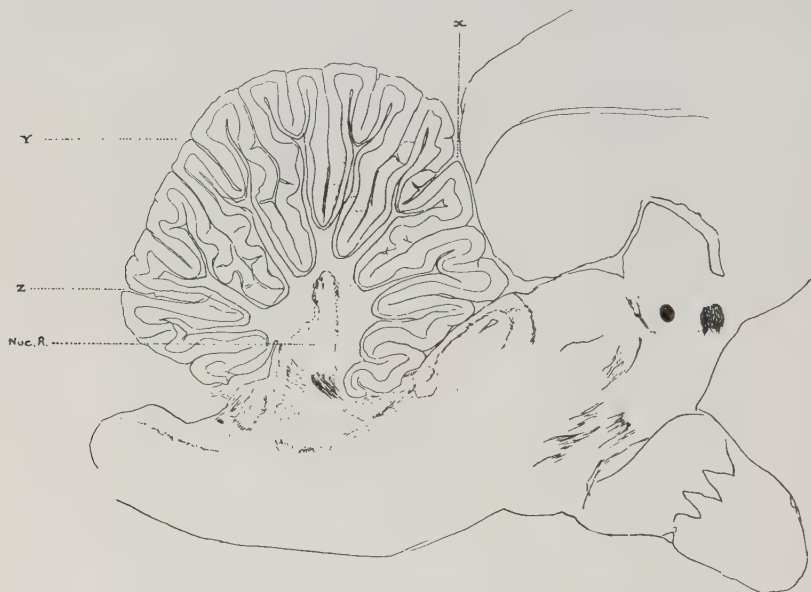


FIG. 62. Median section of cerebellum of turkey. Note the lobulation. *X*, primary fissure; *Y*, prepyramidal fissure; *Z*, fissure uvulonodularis. The lobus medius (between fissures *X* and *Y*) separates the lobus anterior from the lobus posterior. The roof nucleus (*Nuc.R.*) is incorporated within the substance of the cerebellum.

Van Hoeverl describes the cerebellar nuclei of reptiles as genuine cerebellar nuclei, by reason of their connection with the red nucleus through the brachium conjunctivum which is now much better developed than in the lower vertebrates. Furthermore the nuclei receive fibers from the cerebellar cortex. These observations tend to confirm the correlation of the mesial cerebellar nucleus with the roof nucleus of mammals and the lateral with the paleodentate or inter-

mediate nuclei (globosus and emboliformis of mammals). The cortical connection establishes their relation to the vermis.

BIRDS

The lobulation noted in the reptiles is present in the embryo chick and becomes much more elaborate in the adult bird (figs. 60 and 62). Provisions must be made for the new functions of flying and biped locomotion, and for the highly varied and complex posture patterns which they create. These new demands are met by an increase in the lobulation and foliation of the vermis, which is marked anteriorly by the sulcus primarius and posteriorly by the sulcus prepyramidalis (which is secondary); these sulci divide the vermis into lobus anterior, lobus medius and lobus posterior (fig. 62).

The anterior and posterior lobes constitute the oldest parts of the vermis, being the only parts which receive the vestibular fibers, as demonstrated by Ingvar in his experiments on a congenitally deaf cat. This criterion, is in keeping with the principle of cerebellar phylogenesis, that the primitive cerebellum, *i.e.*, the archeparencephalon, is essentially vestibular.

With further development, the anterior lobe divides into four lobules and the posterior lobe into three (pyramis, uvula and nodulus). This lobulation is quite constant, in contrast to the lobus medius, which is probably a more recent acquisition and varies greatly in size and development.

A good deal of light is thrown on the identity of these parts by a study of the spinocerebellar tracts, which closely follow the distribution of the vestibular system (fig. 61). The greater part of the anterior lobe according to Ingvar, receives most of the spinocerebellar fibers, especially the ventral fibers; in this respect it resembles the anterior lobe of the alligator. However, the lingula, which borders on the anterior medullary velum, receives no spinocerebellar fibers and in its topographical relation to the midbrain and velum, recalls the valvula of fishes. Certain it is, that it belongs to the most primitive part of the cerebellum and for that reason is subject to the least variation.

The posterior lobe, which merges laterally with the auricle and embraces the lateral recess, resembles the posterior lobe of the alligator and receives some of the dorsal spinocerebellar fibers. The lobus medius in its most anterior part receives only a very few spinocerebellar fibers (fig 61).

The advance noted in the avian cerebellar organization, is reflected in the highly differentiated cerebellar nuclei which are incorporated within the cerebellum (fig. 62). Mesial and lateral groups are plainly demarcated and readily identified with the roof and the intermediate or paleodentate nuclei of mammals respectively; (fig. 43, *D*) the lateral nucleus is continuous with the large polygonal cells in the tegmentum of the hindbrain, regarded by Shimazono and van Hoeverl as Deiters nucleus; Van Hoeverl also figures a nucleus bigeminis which is possibly the homologue of Bechterew's nucleus in mammals.

MAMMALS

The most striking difference between the cerebellum of mammals and that of the lower vertebrates, is the greater width of the former, due to the development of the cerebellar hemispheres (fig. 63, 64, and 65). The lobulation is also very pronounced (fig. 70).

The evolution from the avian type can be traced through some of the simpler mammalian forms.

The simplest is that of the marsupial mole (*Notoryctes typhlops*). It gives an excellent idea of the fundamental plan of the mammalian cerebellum and as Elliot Smith succinctly states "it represents a stage through which the more complex organ of all other mammals passes at an early stage in the developmental history." A sagittal section clearly demonstrates the rudimentary character of the organ in the mole and in the bat (figs. 67, 68, and 69).

In another transition form, *Echidna* (belonging to the lowest subclass of mammalia), Kappers has pointed out that the cerebellar hemispheres are poorly developed; but the flocculus and paraflocculus are well differentiated and the vermis is clearly divided into the three lobes.

However, the cerebellar hemispheres must be regarded as particular mammalian accessions, which constitute the neocerebellum, each hemisphere consisting of a lobus ansiformis and paramedianus (to use Bolk's terminology) (fig. 65). It is well to think of the cerebellum as a transverse organ, with transverse sulci (fig. 66) running through the substance of the vermis and hemispheres, as if they were one, so that a neocerebellar equivalent is provided for each lobule of the vermis with the exception of the lingula.

As in the avian cerebellum, the anterior lobe of the vermis varies the least and presents usually four lobules. The posterior lobe,

according to Ingvar, can be divided into two parts—a median, consisting of pyramis, uvula and nodulus, and a lateral, part made up of (1) paraflocculus, which is a lateral continuation of pyramis and uvula, and (2) the flocculus, which is a lateral extension of the nodulus.

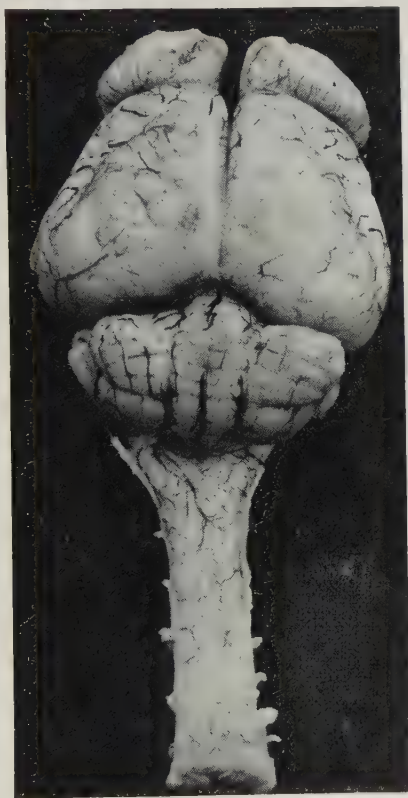


FIG. 63. Dorsal view of brain of armadillo. Note the increase in the transverse diameter of the cerebellum, due to the development of the cerebellar hemispheres (collection of Adolf Meyer).

Edinger and Comolli, regard the anterior and posterior lobes, together with the lobus medius, the oldest parts of the cerebellum. Kappers concurs in this view, and in support thereof cites the ontogenetic studies of Valkenburg, the pathologic studies of H. Vogt and Astwazaturow, and the cases of cerebellar atrophy reported by Brouwer.

However, Ingvar would omit the lobus medius, regarding this part as a more recent acquisition. He bases his opinion on the lower vertebrates, as already noted. In mammals, he found the fibers distributed to the uvula, the nodulus, the lingula and the flocculus, and therefore regarded these structures as the oldest parts of the

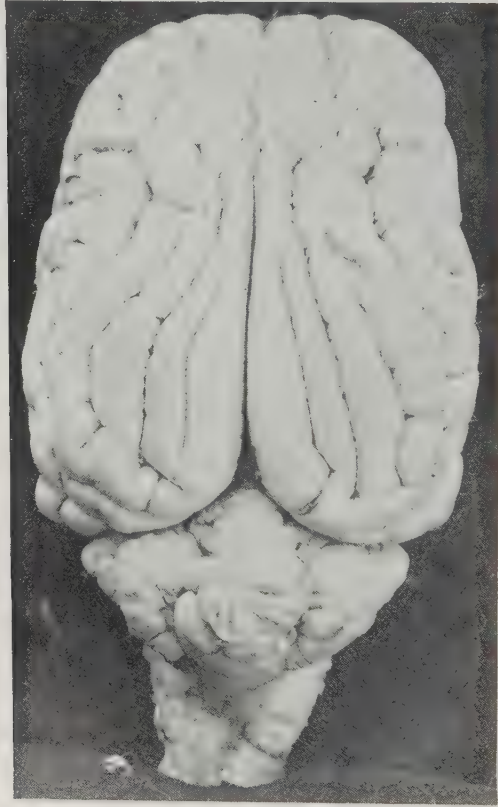


FIG. 64. Dorsal view of brain of deer

cerebellum. This conclusion seems logical and is supported by abundant evidence throughout the vertebrate phylum, bearing on the distribution not only of the primitive vestibular fibers, but also of the spinocerebellar. Apparently, Edinger's concept must be revised.

In mammals, according to Ingvar, and Horsley and McNalty, the spinal cord fibers to the cerebellum are for the most part uncrossed

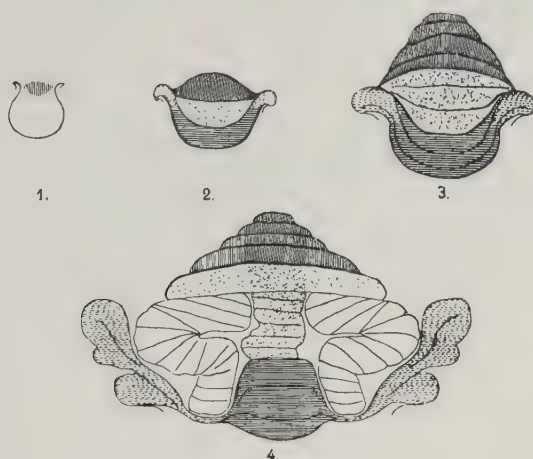


FIG. 65. Schematic representation of the cerebellum. 1, amphibia; 2, crocodile; 3, bird; 4, mammal. Vertical lines, anterior lobe; horizontal lines, posterior with auricular lobe or flocculus; dotted lines, lobus medius; white, lobus ansopara medianus (Ingvar).

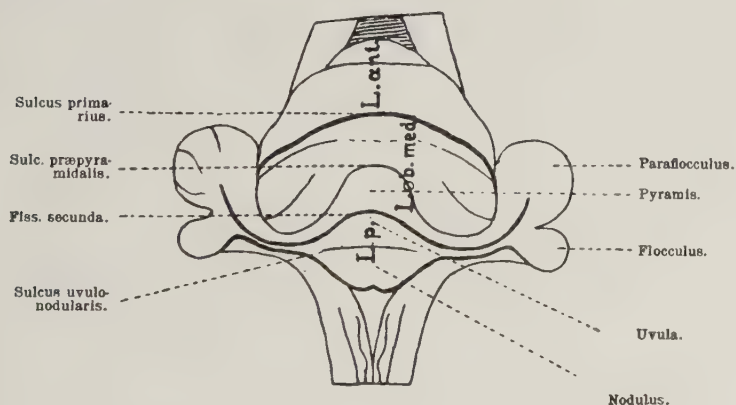


FIG. 66. Schematic representation of the cerebellar lobes and fissures in mammals (Elliot Smith).

and confined to the vermis; the ventral spinocerebellar fibers being distributed chiefly to the anterior lobe, the dorsal partly to the

anterior and the remainder to the posterior lobe. It is pertinent to note, and not without significance, that the lobus medius and the cerebellar hemispheres and the flocculi do not receive any spino-cerebellar fibers.

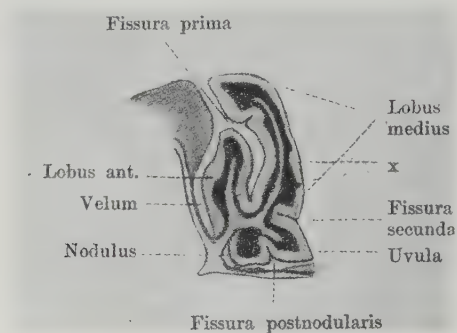


FIG. 67. Sagittal section of cerebellum of marsupial mole

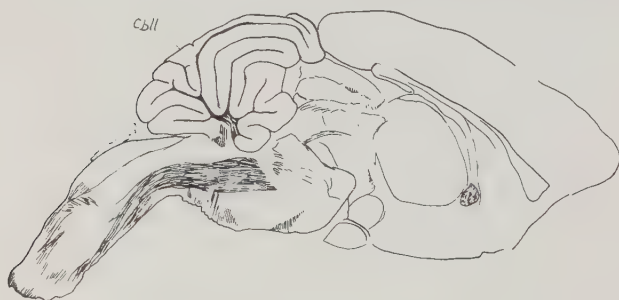


FIG. 68. Median section of brain of mole. Note rudimentary character of lobulation of cerebellum (*Cbl.*).

The principal mammalian contribution to cerebellar evolution, lies in the incorporation of the cerebral hemisphere component. The development of the cortico-ponto-cerebellar system which brings the cerebellum into the forebrain circuit, may be looked upon as an elaboration of the primitive optic and auditory systems described in the lower forms. The connection of the cerebral with the opposite cerebellar hemisphere enables the cerebellum to assume a higher rôle in the sphere of sensorimotor coördination.

With the acquisition of these new structures, the principal or neodentate nucleus makes its appearance and receives fibers not only from the cerebellar hemispheres, but also from the lobus medius and flocculus (fig. 71). The roof and paleodentate nuclei are clearly differentiated and incorporated within the cerebellum; the roof

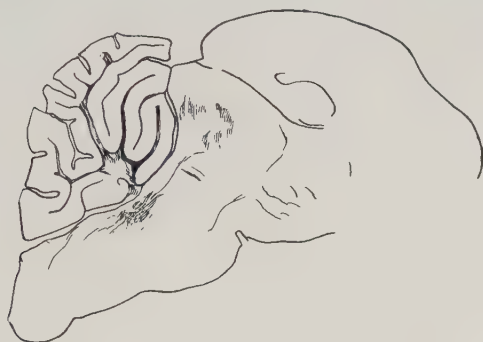


FIG. 69. Median section of brain of bat. Note rudimentary character of cerebellar lobulation.

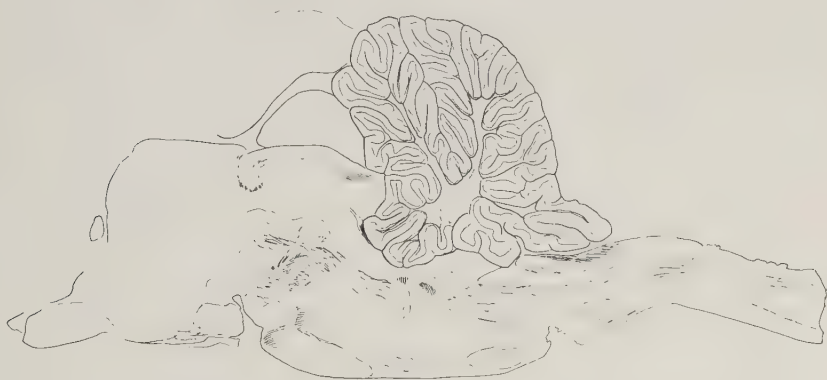


FIG. 70. Median section of cerebellum of squirrel. Note the marked lobulation

nucleus according to Kappers receiving fibers from the anterior lobe.

In association with Dr. S. Hirshfeld, experiments were performed on the fastigial part of the vermis in the cat. I shall not, at this time, go into details, but shall limit myself to a summary of the outstanding findings.

A new approach was used. The usual method of getting at the basal parts of the cerebellum from the surface offers many difficulties and complicates the problem by injuring other structures on the way.

In the animals operated on, the cerebellum was approached through the foramen magnum, the lower pole of the posterior lobe readily uncovered and retracted to expose the roof of the fourth ventricle, containing the cerebellar nuclei. In some of the animals, unipolar

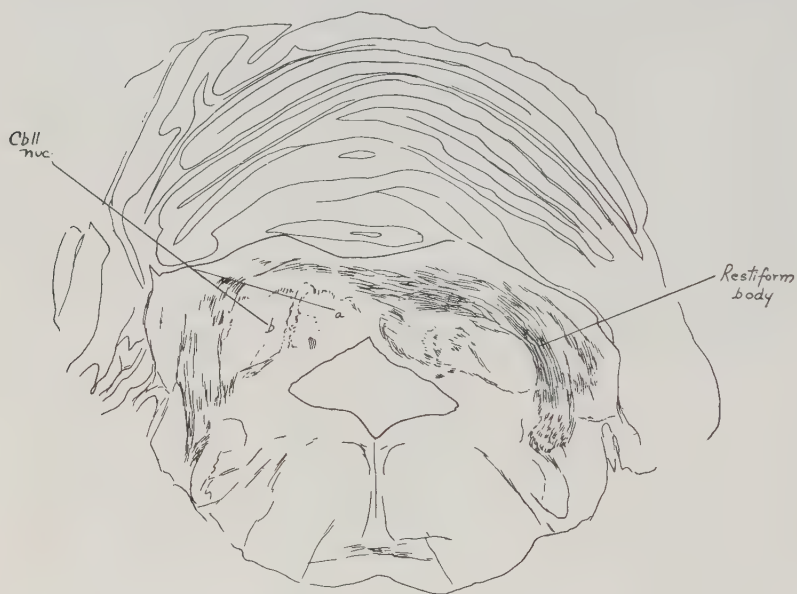


FIG. 71. Transverse section through the cerebellum of a sloth. *Cbl. uc.*, cerebellar nuclei: (a) roof nucleus, (b) dentate nucleus.

faradic stimulation was applied to this region and in others bipolar. The results were the same. The following observations were made: as a result of stimulation with a very weak current—twitching of the eyelids of the same side with occasional closure of that eye; with a stronger current there was usually a spread to the other eye and involvement of the periorbital muscles, also movements of the upper and lower extremities. As a result of the lesions produced, the animals assumed definite postures; they lay on the same side as the lesion and vigorously resisted any attempt to turn them over; some showed a

fine tremor of the head, trunk or homolateral extremities; in attempting to walk the gait was uncertain and decidedly ataxic and after a few steps the animal invariably fell to the same side, although in others circular movements, retropulsion, rotation on the long axis retraction of the head and the attitude of decerebrate rigidity were also observed. After a few days, these disturbances disappeared almost entirely, and the animal continued well. Nystagmus was not observed.

SUMMARY AND CONCLUSION

The study of the phylogenetic development of the cerebellum brings to light definite factors and forces which shape its morphological and physiological patterns. Environmental needs result in the elaboration of certain types of functional activity, which determine the acquisition of new mechanisms for their exercise and expression.

In the lower orders of the vertebrate phylum, the lateral line system and the semicircular canals, represent such specialized acquisitions in response to the demands for finer balancing and more complex postural adjustments. The synthesis of these new streams of impulses, takes place in the cerebellum, which develops in the immediate vicinity of the vestibular mass and serves to mediate its function.

The several classes of vertebrates were studied, including the following species: Petromyzon, Dog Fish, Pike, Frog, Snake, Lizard, Uromastix, Iguana, Turtle, Alligator, Ostrich, Turkey, Kingfisher, Armadillo, Deer, Mole, Bat, Squirrel and Sloth.

Throughout, the plan of cerebellar development is uniform and reveals the same constant topographical relations to the vestibular nucleus, the fourth ventricle and the midbrain.

The basis of cerebellar expansion in all vertebrates is the fundamental cerebellar arch, spanning the roof of the fourth ventricle, with each end rooted in the vestibular area of the middle hindbrain segment. It occurs in most rudimentary form in cyclostomes and amphibia, as archeparencephalon. It is constant in all forms and in the human is represented by the connection of the vestibular nuclei with the vermis and roof nuclei, *i.e.*, the inner cerebellar arm.

The vestibular nuclei constitute the segmental foundation, from which the cerebellum is evolved as a suprasegmental organ, reflecting in its early development both the differentiation of vestibular and lateral line functions and the influence of the optic lobes. Its sub-

sequent evolution is determined by the development of the spinocerebellar and corticopontine systems.

The vestibular and lateral line influence is most marked in the cyclostomes, amphibia and fishes. In *Petromyzon* the cerebellum is very rudimentary being hardly more than a commissure between

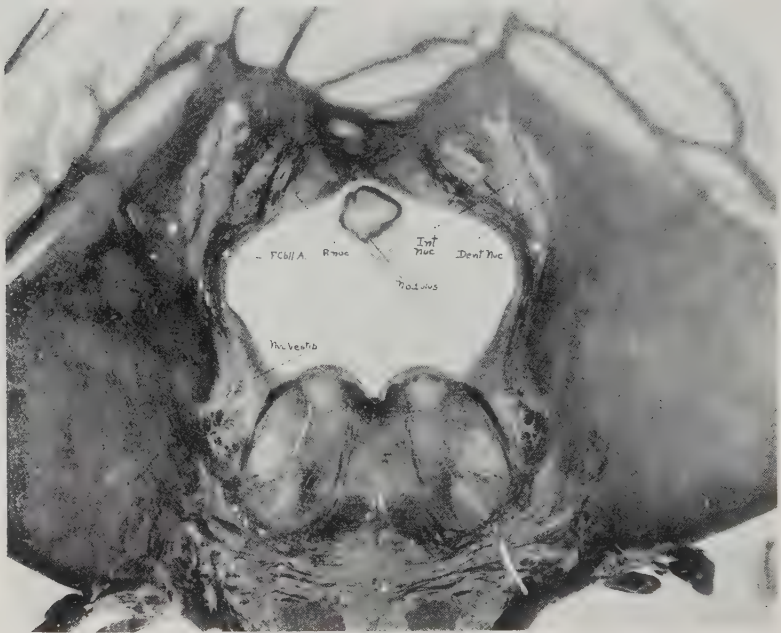


FIG. 72. Transverse section through the cerebellar nuclei of adult human brain. *R.nuc.*, roof nucleus; *Int.nuc.*, intermediate nuclei or paleodentate (globosus and emboliformis); *Dent.nuc.*, dentate nucleus; *F.Cbl.A.*, fundamental cerebellar arch or tractus nucleo-cerebellaris.

the octavolateral areas. This type of cerebellum occurs in those vertebrates that are limbless, namely the snake, *anniella nigra* etc.

The cerebellum of fishes represents a distinct departure from the main line, in the peculiar character of its expansion. However, the three different types that are recognized have the fundamental cerebellar arch in common. In Elasmobranchs, the latter gives rise to a lateral prolongation, the auricular lobe, which is present to a greater or less degree in all the higher vertebrates; it eventually becomes the

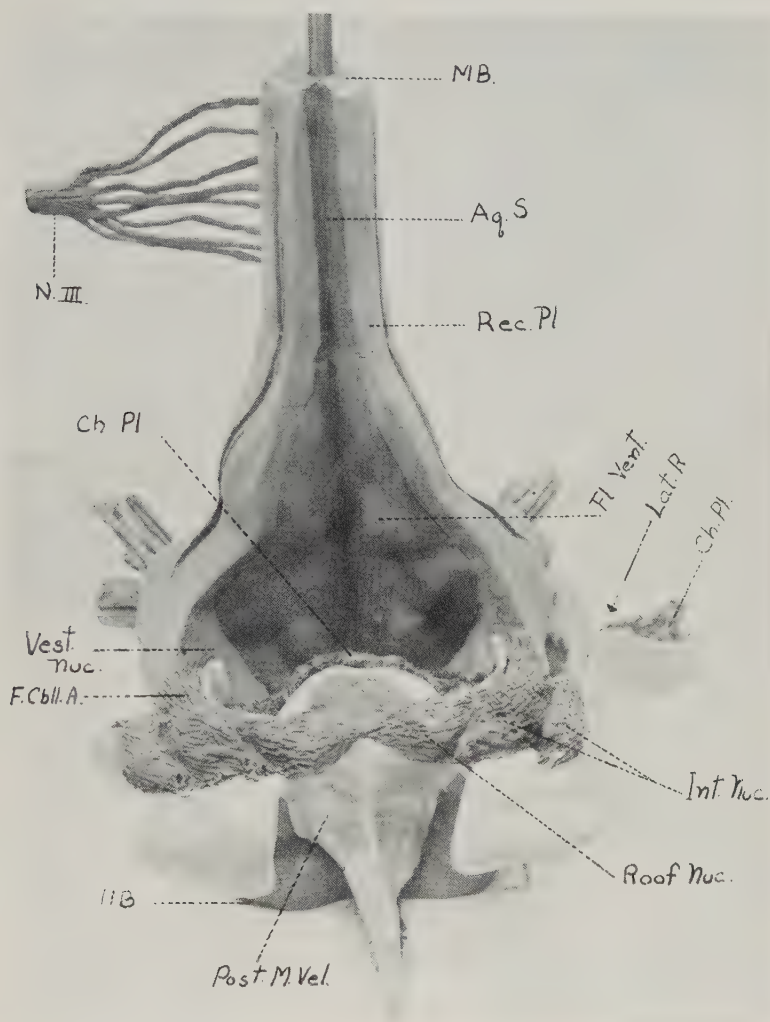


FIG. 73. Dorsal view of reconstruction of floor of fourth ventricle and fundamental arch of the cerebellum of adult human brain. This view is equivalent to that of the brain stem with the colliculi and cerebellum removed. *MB.*, cephalic limit of the midbrain; *HB.*, caudal limit of the hindbrain; *N. III.*, oculomotor nerve; *Aq. S.*, floor of aqueduct of Sylvius; *Rec. Pl.*, receptor plate (or alar lamina); *Fl. Vent.*, floor of fourth ventricle; *Lat. R.*, opening of lateral recess with choroid plexus (*Ch. Pl.*); *Vest. nuc.*, vestibular nucleus; *Post. M. Vel.*, posterior medullary velum. The roof and intermediate nuclei (*Int. Nuc.*) lie in the path of the fundamental cerebellar arch (*F. Cbl. A.*).

flocculus in mammals. Another new structure appears in the midline, as the evaginated dorsal median body, superimposed on the fundamental arch and its growth determined by the acquisition of the lateral appendages and the development of the spinocerebellar tracts.

In Ganoids the cerebellum is much less expansive and presents a new structure, the valvula, which arises in the midline as a cephalic invagination of part of the fundamental arch. It is concerned essentially with lateral line function.

The cerebellum of Teleosts represents a composite of the Elasmobranch and Ganoid types. It contains all the new structures: the evaginated dorsal median body, the invaginated valvula and the auricular lobes.

The diversity of cerebellar pattern in the different fishes, is related to the distribution of the various systems. The fundamental arch with its prolongations (the valvula and the auricles) is connected with the vestibular and lateral line fields; the dorsal median evagination, which synergizes the intersegmental body movement with the lateral appendages and is concerned with the execution of inherent automatic associated movements, represents the spinocerebellar field, together with the optic and other somesthetic components.

The cerebellum of amphibia, which reflects the transition from aquatic to terrestrial life, reverts to the *Petromyzon* type, although in the frogs, the lateral line system drops out at the time of metamorphosis. However, functionally, the cerebellar apparatus of the latter is characterized by the greater development of the vestibular and spinocerebellar systems. The cerebellum and vestibular nucleus have functions in common, similar to those of the semicircular canals, although the cerebellum itself also synergizes body and limb movements.

In reptiles, this coördination of the body with the extremities assumes a very important part in determining the cerebellar pattern. There are wide variations in the different forms depending upon the type of motor progression. A distinct advance is noted in the everted cerebellum of the lizard family, which gives evidence of transverse fissure formation that goes on to lobulation in the cerebellum of the alligator.

The internal cerebellar structure of the lizard group is distinguished by a projection of the granular layer into the Purkinje zone. In *Iguana* and *Uromastix* this projection is very marked and appears to

be homologous with the primary sulcus described by Elliot Smith in mammals. I was able to trace and identify this structure also in the cerebellum of the frog. So that even at this early stage, there is an indication of fissuration.

The lobulation noted in reptiles is further elaborated in the avian cerebellum, to provide for the new functions of flying and biped locomotion. The primary sulcus and the sulcus praepyramidalis divide the vermis into anterior, middle and posterior lobes, which are homologous with those of mammals.

The most striking difference, between the cerebellum of mammals and the lower vertebrates, is the greater transverse axis of the former, due to the development of the cerebellar hemispheres, in conjunction with the corticopontine system. Of the lobes of the vermis, the anterior and posterior constitute phylogenetically the oldest part of the cerebellum and receive the spinocerebellar system. The lobus medius may be considered as neovermis.

The relation of the cerebellum to the vestibular nuclei, is also reflected in the differentiation of the cerebellar nuclei, which develop from a very rudimentary form in close connection with the primitive vestibular mass.

In *Petromyzon*, these parts are represented by a group of cells in the dorsolateral area of the hindbrain, which receives vestibular and lateral line fibers. In this area, Deiters' nucleus and the primitive nucleus cerebelli develop practically as one mass in the hindbrain tegmentum, the latter giving rise to fibers which are the equivalent of the superior cerebellar arm in higher vertebrates. The same relationship is seen in fishes and amphibia. Further differentiation of the nuclei takes place in the reptiles. The cerebellar nuclear mass has shifted dorsally and can be divided into mesial and lateral parts. The mesial nucleus represents the roof nucleus of mammals; the lateral group of cells which is continuous with the vestibular nucleus, probably represents the oldest part of the dentate nucleus, *i.e.*, the paleodentate or the intermediate nuclei (globosus and emboliformis) of higher vertebrates. In this connection the old concept of the dentate nucleus needs to be revised. It must be studied in terms of a phylogenetically older part (paleodentate) and a more recently acquired portion (neodentate), which appears first in the mammals with the development of the cerebellar hemispheres.

As we ascend the vertebrate scale, there is a definite shifting of the cerebellar nuclei dorsally, until in the birds and in the higher forms they are definitely incorporated within the cerebellum itself.

Lesions of these parts in the vermis of the cat produced ataxia of the extremities, definite postural defects and forced movements which lasted but a few days.

In conclusion, it should be noted that the study of cerebellar phylogenesis makes it evident that the principle of cerebellar construction is the same throughout the vertebrate phylum. The pattern, in many respects is almost identical. The evolution of the cerebellum parallels that of the body itself, in its various stages: first, the development of the axial body, later the development of lateral appendages, then the coördination of these parts, leading eventually to the liberation of the extremities and their independent use, for purposes other than locomotion.

This elaboration and specialization of structure is physiologically determined and leads to the high morphological position which the cerebellum has attained.

DISCUSSION

The following question submitted to Dr. Hausman before the Commission, together with the answer to it, is here reported verbatim.

PROF. FREDERICK R. MILLER: I should like to ask Dr. Hausman, whether in his experimental removals, he noticed any changes in tone as a result, and also whether he noticed an increase in activity or the phenomenon of exaltation? We know that Rademaker, in Magnus' laboratory in Utrecht, denies that atonia resulted from removal of the cerebellum. At first they obtained atonia or hypertonia, but afterward, in the later stages, they deny it.

DR. LOUIS HAUSMAN: I found in such animals that the extremities on the same side as the lesion usually were hypotonic, but this hypotonia did not persist very long; in fact, the various disturbances which occur in these animals disappear within a few days. To my own satisfaction I think I demonstrated that the same side did show some degree of hypotonia, although slight. However, the exaltation or "dynamic" phenomena originally noted by Luciani were very striking and presented for a few days, even though the lesions produced were very small and limited to the fastigial part of the vermis. This period was characterized by forced movements, retraction of the head and posture resembling decerebrate rigidity, in addition to the other phenomena that I have already noted.

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CHAPTER IV

THE MEASUREMENT OF THE HUMAN CEREBELLAR SURFACE¹

WALTER M. KRAUS, M.D., AND ARTHUR WEIL, M.D.

IN A communication to the American Neurological Association in June, 1926, Kraus and Ditto described a method of measuring the cerebral and cerebellar surfaces (1). In this communication it was stated that Kreuzfuchs (2) is the only author whose work dealt with the surface area of the cerebellum. In 1902 he estimated this for one case only. He emphasized the great number of errors that might occur. His method was to clear with aniline oil and to draw the grossly cut cerebellum with the aid of an Edinger drawing machine. He estimated the length of the lines obtained with a curvometer. He estimated the surface to be 84,246 sq. mm., of which 16,344 (19.4 per cent) was visible. Comparing these figures with those of Wagner and Henneberg, we find that the relation of the total surface of the cortex to the total surface of the cerebellum is 2.6:1 in man. It is interesting in passing to quote Kreuzfuch's estimation of the number of Purkinje cells which he sets at 14,237,674.

The present communication shows that these observations of Kreuzfuchs were inaccurate insofar as total surface is concerned. A value for the total surface of the cerebellum which was close to his own figures was obtained when the sections were drawn at low magnification without taking the finer lobulation of the cerebellar convolutions into consideration. The value obtained was 81,100 sq. mm. In drawing at higher magnification and following the outlines of the figures with a hand lens much higher values were obtained.

This communication also presents in broad outlines some newer aspects of cortico-mensuration and data showing the actual values and relations of visible and total surface of one human cerebellum.

The details of the technique of preparing the brain for measuring, the technique of the measuring and the details of the mathematics

¹ From the Neuropathological Laboratory, Montefiore Hospital, New York.

TABLE I
PERIMETERS IN CENTIMETERS

SECTION NUMBER	LEFT HEMISPHERE		RIGHT HEMISPHERE		VERMIS		REST*	
	Visible	Total	Visible	Total	Visible	Total	Visible	Total
30	4.3	8.6	6.4	24.4				
40	5.1	11.6	8.5	40.2				
50	5.5	11.8	8.7	41.5				
60	6.6	13.3	11.0	54.0				
70	9.2	38.2	10.5	75.0				
80	11.9	52.0	10.8	79.0				
90	11.1	74	11.5	95				
100	11.4	85	12.1	95				
110	12.0	83	12.4	90				
120	12.4	96	12.4	95				
130	11.2	107	11.2	89	1.5	1.5		
140	11.7	97	11.5	79	4.3	8.6		
150	12.0	81	12.0	94	4.8	11.5		
160	12.4	80	12.8	87	5.4	13.0		
170	12.7	83	12.7	80	5.0	13.2		
180	12.8	77	12.7	77	5.2	16.7		
190	12.9	78	13.7	76	6.4	16.1		
200	12.6	75	13.1	82	6.2	15.9		
210	11.3	85	13.3	89	4.7	13.6		
220	12.5	94	13.7	99	3.8	16.4		
230	13.0	97	13.0	96	3.8"	15.2		
240	13.0	107	13.0	95	2.5	5.8		
250	12.4	115	12.4	108	2.1	7.7		
260	11.9	113	11.6	107	1.7	8.3		
270	11.3	112	12.2	104	1.4	15.2		
280	11.4	113	11.7	103	2.0	16.3		
290	11.3	111	11.7	103	3.5	18.4		
300	10.8	107	11.0	98	3.0	22.2		
310	10.3	104	10.3	92	3.9	18.9		
320	10.5	99	10.2	89	3.6	18.5		
330	10.6	96	9.8	76	3.1	19.3		
340	10.5	83	9.7	63	2.6	16.8		
350	9.5	61	7.8	48	2.0	16.1		
360	6.0	26	6.9	37	2.6	17.5		
370							11.2	61
380							11.4	51
390							9.3	37
400							7.4	25
410							5.3	8

* "Rest" are the most cranial sections of the cerebellum in which the separation into hemispheres and vermis could not be accomplished.

involved in arriving at the final conclusions will be presented in another paper (3). The formula for determining the surface area given in the first communication (1) was used in a somewhat different manner in that s , the slant height between sections, was determined graphically rather than mathematically in calculating the visible surface. In addition, it was decided to assume that the outlines of the cerebellar sections approached the form of a truncated cone or a sphere more nearly than a pyramid. The perimeters of the cerebellum were converted into the circumferences of cones and the small circles of spheres. The difference between the two latter is

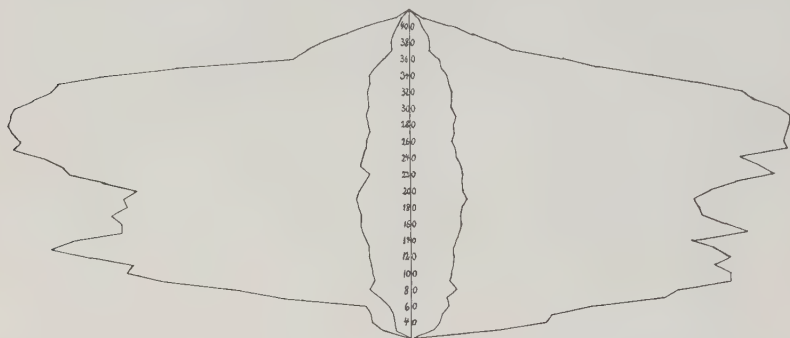


FIG. 74. Graphic representation of the perimeters of the visible surface and the total surface of the cerebellum. The perimeters found in each tenth section were reduced to one-fifth the length and projected on the horizontal line of the millimeter paper. The height between two sections was taken at 0.5 mm. and drawn on the vertical line. The inner contours represent the visible surface, the outer contours the total surface of the cerebellum.

only 2 per cent and too small to make it necessary to use the more complicated graphic technique for the sphere. We believe the truncated cone to be the more accurate way to determine the surface.

Next, the perimeters of each section, the visible as well as for the total surface, were projected on cross section paper at a reduction of one-quarter of the original value. The distance between two sections was 5 mm. In this way one may obtain a graphical representation of the relation between visible and total surface. The value for this relation may either be found by measuring the planes enclosed in the two circumferences (fig. 74) with a planimeter or by adding all the perimeters of the different sections and dividing the sum of the pe-

rimeters of the total surface by those of the visible. The relation found was 1:6.67 for the cerebellum. The absolute value for the total surface was then obtained by multiplication of this relation with the absolute value of the visible surface as found above.

An attempt was then made to measure the total surface of the cerebellum. A human cerebellum which was preserved in 95 per cent alcohol was divided into two equal halves. Next the meninges were removed and each lobulus was carefully separated. Finally, a number of lobuli were obtained which resembled cylindrical rods. With the help of a hand lens and a caliber, the different diameters of these rods were measured and their frustrum calculated as the

TABLE II
SURFACE IN SQUARE CENTIMETERS

	FORMULA OF TRUNCATED CONE		RATIO OF VISIBLE TO TOTAL SURFACE
	Visible	Total	
	<i>sq. cm.</i>	<i>sq. cm.</i>	
Left hemisphere.....	68.64	480.7	1:7.00
Right hemisphere.....	70.47	503.4	1:7.14
Vermis.....	12.87	52.5	1:4.08
Rest.....	9.25	37.8	1:4.08
Total surface of cerebellum.....	161.23	1074.48	1:6.67
Kreuzfuchs.....	163.44	842.46	1:5.16

frustrum of a cylinder or an ellipsoid. The different values were added and for the left half of the cerebellum 59,292 sq. mm. were obtained. Assuming that the right half was equal to the left, the value for the total surface of this cerebellum would be 118,580 sq. mm. In applying these figures one should always bear in mind the roughness of this method, though, as will be shown below, they very nearly approach the more exact figures of the actual measuring.

A problem which must be considered when calculating the cerebellar surface is the amount of shrinkage which takes place during the different steps of embedding the brain. As will be shown in another paper (4), the loss of surface of the fresh brain was found to be approximately 9 per cent. This difference has to be added to the figures obtained from the serial sections.

A normal brain from a man forty-two years of age who died from bronchopneumonia, was sectioned serially and horizontally. Each tenth section was stained with the Loyez Method and measured (fig. 75.)

Table I gives the results for every tenth section. An attempt was made to separate the cerebellum into its two hemispheres and the vermis. Naturally, this attempt is very incomplete. Nevertheless, the figures for this separation are given below, in order to give an

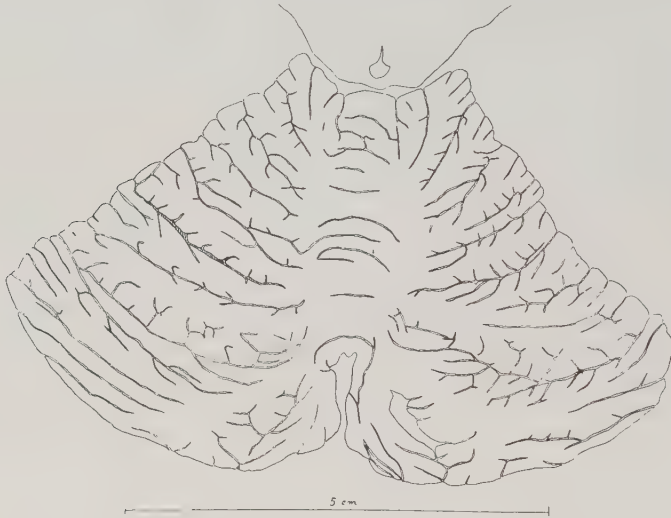


FIG. 75. India ink drawing of a horizontal section through cerebellum used for measuring.

approximate idea of the relationship between these two structures. The flocculi are added to the hemispheres.

Table II gives the figures for the surfaces of the different parts of the cerebellum and the relation of visible to total surface.

SUMMARY

Calculation of the total surface of the cerebellum of a man forty-two years of age, measured at every tenth section of 100 micra each, yields a result of 107,440 sq. mm. (1074.4 sq. cm.); calculation of the visible surface, 16,120 sq. mm. or 15 per cent of the total surface. The

relation of visible to total surface is 1:6.67. There is a greater total surface in relation to visible surface in the hemispheres than in the vermis.

The visible and total surfaces of the right hemisphere are larger than those of the left. In the cortex this has been found (in the same brain) to be the reverse.

As only every tenth section was measured, we believe that the results are too low, as a result of not including measurement of fissures between each tenth section.

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CHAPTER V

THE STRUCTURE AND DEVELOPMENT OF THE PROPRIOCEPTORS

ADOLPH ELWYN, M.D.

IN THE general receptive field there is a group of sensations through which we become aware of the various locomotor changes, such as the movement of the joints, as well as the changes in the form and tension of the muscles. By means of these sensations we are able to recognize with remarkable accuracy, even when blind-folded or in total darkness, a given position or change of position of the whole body or of any of its parts, and to produce efficiently any desired movement. This "locomotor" sense is independent of cutaneous sensation, and there is ample clinical and experimental evidence that there may be complete loss of the latter, without any, or only slight, interference in the recognition of locomotor changes. Anatomically these sensations are represented by a group of complicated end-organs or receptors found in both the active and passive portions of the locomotor apparatus. They are the proprioceptors of Sherrington, which perhaps should more specifically be called the "locomotoceptors" or sense organs of the locomotor system.

This group of end-organs comprises the neuro-muscular spindles within the muscle itself; the neuro-tendinous organs of Golgi in the tendons, periosteum and perifascicular tissue; and the corpuscles of Pacini or similar modified bodies found in the joints and to a varying extent also in the periosteal and perimyseal connective tissue. It is the purpose of this paper to present the present knowledge of the structure and development of these receptors which have a remarkably wide distribution in the vertebrate phylum. Other more simple arborizations of isolated nerve fibers, which Giacomini, Dogiel, and others have described as occurring at the junction of muscle and tendon, have not been included in this consideration.

The paper is based largely on the investigations of a number of workers, and especially on those of Kerschner, Golgi, Ruffini, Sherrington, Batten, Cipollone, Cattaneo, Ciaccio, Huber and deWitt, Dogiel,

Cilimbaris and Tello. The embryology is in the main an account of the recent comprehensive work of Francisco Tello. An extensive bibliography is appended.

THE NEURO-MUSCULAR SPINDLES (FIGS. 76, 5, 77, 6-10, 78, 11 AND 12)

Historical

Hassal (1851) and Rollet (1856) observed in muscle the presence of slender fibers which were morphologically different from ordinary muscle fibers. Even earlier, Miescher (1843) found peculiar bodies in the musculature of the mouse, which he termed "Muskelschläuche," and similar bodies were found by Siebold (1853) in the rat. While these observations probably referred to the muscle spindles, the first detailed account of these sense organs was furnished by Weissmann in 1861. He describes in the muscles of the frog, bundles of slender muscle fibers in groups of six, eight, or more, wound about in the center by a cord, and enveloped by a granular substance, making it difficult to trace the individual fibers. Apparently the fibers extended from tendon to tendon. He believes these fibers to represent stages in the development of muscle.

In the next few years Koelliker (1862) and Kuehne (1863) made a thorough study of these structures in the muscles of the frog and white rat respectively. In these and subsequent papers they added important structural data, and introduced specific names, the "muscle buds" of Koelliker and the "muscle spindles of Kuehne." The buds or spindles are fusiform or nodular bodies consisting of a bundle of slender muscle fibers of embryonal appearance. They are supplied by nerves coming from a common trunk, the sheath of the nerve passing into the sheath of the spindle. The nerve fibers undergo division and often appear wound up in a coil. The muscle fibers are more slender than ordinary fibers, show a well-marked though coarser striation near the end, but lose these in the center which is filled by a large number of round, pale staining nuclei. Both investigators conclude that these bodies are related to the development and growth of muscle. Beale (1862) holds to the same view.

Besides the work of Peremescho (1863) no further papers were published on the subject for the next dozen years or so. But from 1874 to 1892 the literature is flooded by the records of numerous observations and investigations, of which the most important ones

are those of Sachs (1874), Bremer (1883), Mays (1884), Roth (1887), Felix (1888), Kerschner (1888), Cajal (1888), Dogiel (1890), Trinchese (1891), Christomanos and Stroessner (1891), and Thanhofer (1892). While these investigations yielded additional facts regarding the general structure and distribution of the spindles, they failed to distinguish the various modalities of the entering nerves and the exact nature of their end arborizations.

Concerning the significance of the spindles, there was a great deal of conjecture and dispute. Some investigators (Ranvier, Kraske, Bremer, Felix, von Franque) agreed with the view of Kolliker and Kuehne. On the other hand, a number of clinical workers who had noted the constant presence of the spindles in atrophied muscle, believed them to be pathological structures. To this group belong Eisenlohr (1876), Fraenkel (1878), Millbacher (1882), Babinsky (1884) and Eichhorst (1888). Babinsky however changed his opinion in a later paper. As late as 1890 this view was still held by Santesson in the description of the muscle spindles found in a case of myopathy.

The sensory nature of the spindles was first suggested by the experimental work of Sachs (1874). He cut the anterior roots in the frog and after eight weeks, when complete degeneration of the motor fibers had occurred, he observed the presence of two broad, well formed nerves which entered the spindle and wound spirally around it. In 1888, Cajal published a careful drawing of the spindle, in which both sensory and motor endings are definitely indicated. In the same

FIG. 76

1 Inception of neuro-muscular spindle in chick embryo of eleven days' incubation (after Tello). *a*, myofibers; *b*, intrafascicular connective tissue; *c*, fiber which will form sensory ending; *d*, innervated muscle fibers (Weissmann's bundle).

2. Early neuro-muscular spindle in chick embryo, after eleven days' incubation (after Tello). Lettering same as in figure 76, 1.

3. Neuro-muscular spindle in chick embryo of twelve days' incubation (after Tello). Lettering same as in figure 76, 1.

4. Neuro-muscular spindle in human foetus of six months (after Tello). *a*, thick nerve fiber giving rise to ivy or flower-like sensory ending (*c*) in region where bubble masses are found; *b*, thick fiber supplying claw-like or annular ending (*d*); *e*, motor fibers destined to form end plates; *f*, capsule; *g*, thin vaso-motor fibers.

5. Neuro-muscular spindle from cat (after Ruffini). *a*, entering nerve fibers; *b*, flower-like sensory endings; *c*, annulo-spiral sensory ending; *d*, motor fibers with end plates (*e*); *f*, intrafusal muscle fibers; *g*, capsule.

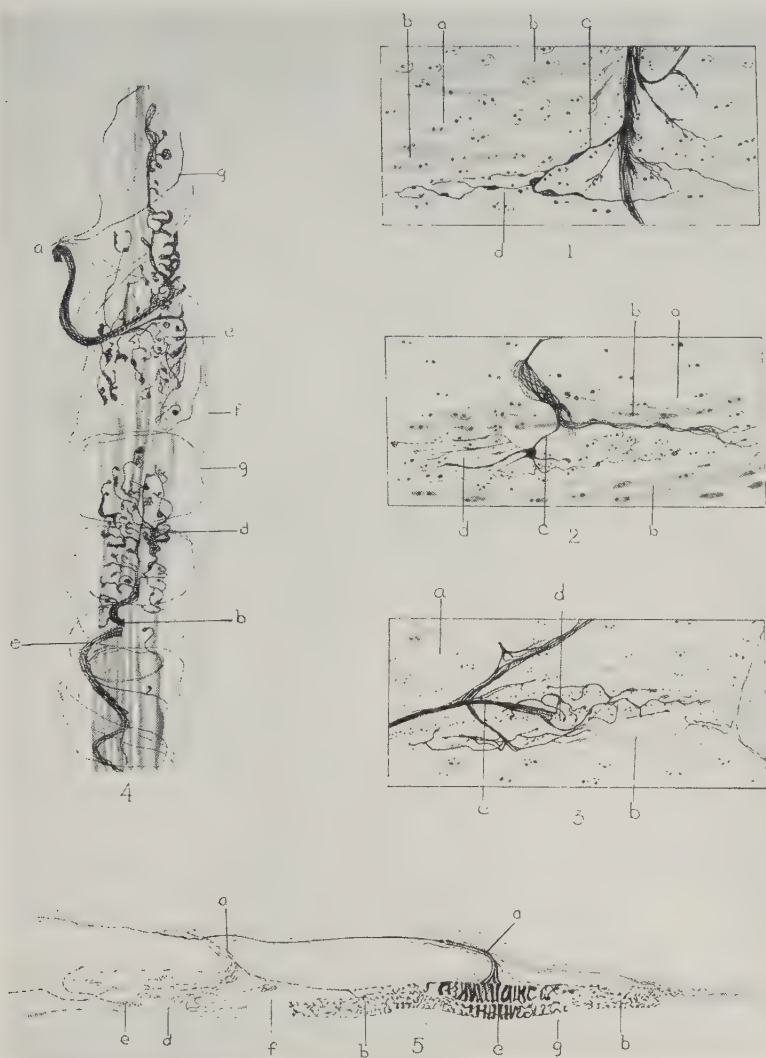


FIG. 76

year there appeared the interesting paper of Kerschner who describes the spindles and suggests that they are sense organs which subserve muscle sense. In a later publication (1892) he compares them with other sense organs in tendons and joints, and in support of their sensory nature puts forward the following points: their abundant nerve supply; the type and richness of their end arborization; the presence of nuclear groups, similar to those found in end bulbs; the frequent ending of part of the same nerve in a tendon organ; and their constant presence and large number in many muscles in which fine muscular sense is needed.

From 1892 there is complete unanimity in considering them sensory organs, and the work of the various investigators is largely centered on the nature of the terminal arborizations of the spindle nerves. Ruffini (1893) was the first to describe and give beautiful illustrations of the exact terminations of the various nerve endings in the cat. His work was extended and completed by the researches of Foster (1894), Sihler (1895), Weiss and Dutil (1896), Batten (1897), Cipollone (1897), Huber and deWitt (1898), Dogiel (1902), and more recently by those of Cilimbaris (1910) and Tello (1917).

Experimental proof of the sensory nature of the spindle fibers, already indicated by the work of Sachs (1874) and Onanoff (1890), was definitely furnished by Sherrington (1895). He examined muscle in which all the motor fibers had been divided and the muscle fully degenerated, and found that the nerve fiber passing to the spindle was well preserved and could be traced to the sensory roots. The later experimental work of Batten (1897) and Cipollone (1898) confirm Sherrington's findings.

At the present time the older theories concerning the function of the muscle spindles, have only a historical interest. These spindles are regarded by all as sense organs equipped with an end-arborization of remarkable extent and complexity.

Structure and distribution

The neuro-muscular spindles are found, from the fourth month of foetal life, in practically all muscles, including the extrinsic muscles of the tongue (Forester, Langworthy), the oculomotor muscles (Cilimbaris) and at least in some extrinsic laryngeal muscles (Forester). They have not been demonstrated in the diaphragm nor in most of the intrinsic tongue muscles. Their number varies in different

muscles, being more numerous in the active muscles of the extremities, especially in the hand, than in those of the trunk. They are very abundant in the eye muscles of the sheep and some related forms (*Cilimbaris*). The number of spindles in individual muscles has been estimated or counted in many instances and are given in table III. The most accurate figures are those of Cipollone, Huber, and *Cilimbaris*.

TABLE III
THE NUMBER OF SPINDLES IN INDIVIDUAL MUSCLES

MUSCLE	NUMBER OF SPINDLES	ANIMAL	AUTHOR
Omohyoideus.....	15	Child, 4 years	Koelliker
Biceps.....	79	Human foetus	Felix
Sartorius.....	8	Rat	Morpurgo
Omohyoideus.....	7	Man	Forster
Genioglossus.....	13	Man	Forster
Hyoglossus.....	6	Man	Forster
Pterygoideus.....	19	Rabbit	Cipollone
Masseter.....	40	Rabbit	Cipollone
Intercostal, 11th space.....	28	Cat	Huber
Intercostal, 12th space.....	18	Cat	Huber
Intercostals (1st six spaces).....	60-100	Cat	Huber
External rectus.....	281	Sheep	<i>Cilimbaris</i>
Inferior rectus.....	175	Sheep	<i>Cilimbaris</i>
Superior rectus.....	148	Sheep	<i>Cilimbaris</i>
Internal rectus.....	96	Sheep	<i>Cilimbaris</i>
Superior oblique.....	108	Sheep	<i>Cilimbaris</i>
Inferior oblique.....	78	Sheep	<i>Cilimbaris</i>
Lev. palpebrae super.....	23	Sheep	<i>Cilimbaris</i>
Retractor bulbi.....	20	Sheep	<i>Cilimbaris</i>

The position of the spindles within the muscle is as variable as their number. They are not only found near tendinous ends (Koelliker, Cattaneo), but also in the fleshy part, often near aponeuroses and intermuscular septa. Several may lie end to end forming a chain of spindles, each with its own nerve supply. In some muscles they are more abundant in the belly, in others near the tendinous insertion. While apparently distributed in a haphazard manner in most muscles, they show a characteristic position in the muscles of the eyeball (*Cilimbaris*). In these band-like muscles the spindles are arranged

near the periphery of the convex surface, forming a sort of cortex, but are completely absent on the concave side. An exception is noted in the superior oblique whose cross section is nearly circular. Here the spindles are distributed along the whole periphery. Cilimbaris found no spindles near the tendinous ends of the muscles.

TABLE IV
SPINDLE MEASUREMENTS OF VARIOUS INVESTIGATORS

INVESTIGATOR	DIMENSIONS OF SPINDLES IN MILLIMETERS		ANIMAL
	Length	Thickness	
Koelliker.....	6.5 - 7.4	0.009-0.042	Child, 4 years
Christomanos and Stroessner....	0.8 -13.0	0.046-0.26	Man
Sherrington.....	0.75- 4.0	0.08- 0.2	Cat, Monkey
Batten.....	0.3 -11.7	0.15 -0.4	Man
Forster.....	0.8 -10.4	0.1 -0.15	Man
Baum.....	2.0 -10.0	0.08 -0.4	Man
Cilimbaris.....	0.05-12.4	0.042-0.16	Sheep

The recorded dimensions of the spindles fluctuate enormously, the extremes being 0.05 to 13 mm. for length and 0.04 to 0.4 mm. for thickness. Batten reported a human spindle 11.7 mm. long, Christomanos and Stroessner one of 13 mm. The more usual length is 2 to

FIG. 77

6. Longitudinal section through external rectus muscle of sheep showing muscle spindle (after Cilimbaris). *a*, outer capsule; *b*, inner capsule; *c*, periaxial lymph space with protoplasmic network; *d*, intrafusal muscle fibers.

7. Muscle spindle from external rectus muscle of sheep; orcein-resorcin fuchsin preparation (after Cilimbaris). *a*, intrafusal muscle fibers; *b*, spiral elastic fibers; *c*, periaxial lymph space.

8. Transverse section of muscle spindle from external rectus muscle of sheep (after Cilimbaris). *a*, inner capsule; *b*, periaxial lymph space; *c*, outer capsule; *d*, intrafusal muscle fibers; *e*, nerve trunk in capsule.

9. Portion of spindle from superior oblique muscle of sheep, showing anastomosis of intrafusal muscle fibers (after Cilimbaris). *a*, lymph space; *b*, capsule; *c*, intrafusal muscle fibers.

10. Muscle spindle from internal rectus muscle of sheep (after Cilimbaris). *a*, flower-like ending; *b*, annulo-spiral ending; *c*, motor plates; *d*, *e*, entering sensory fibers.

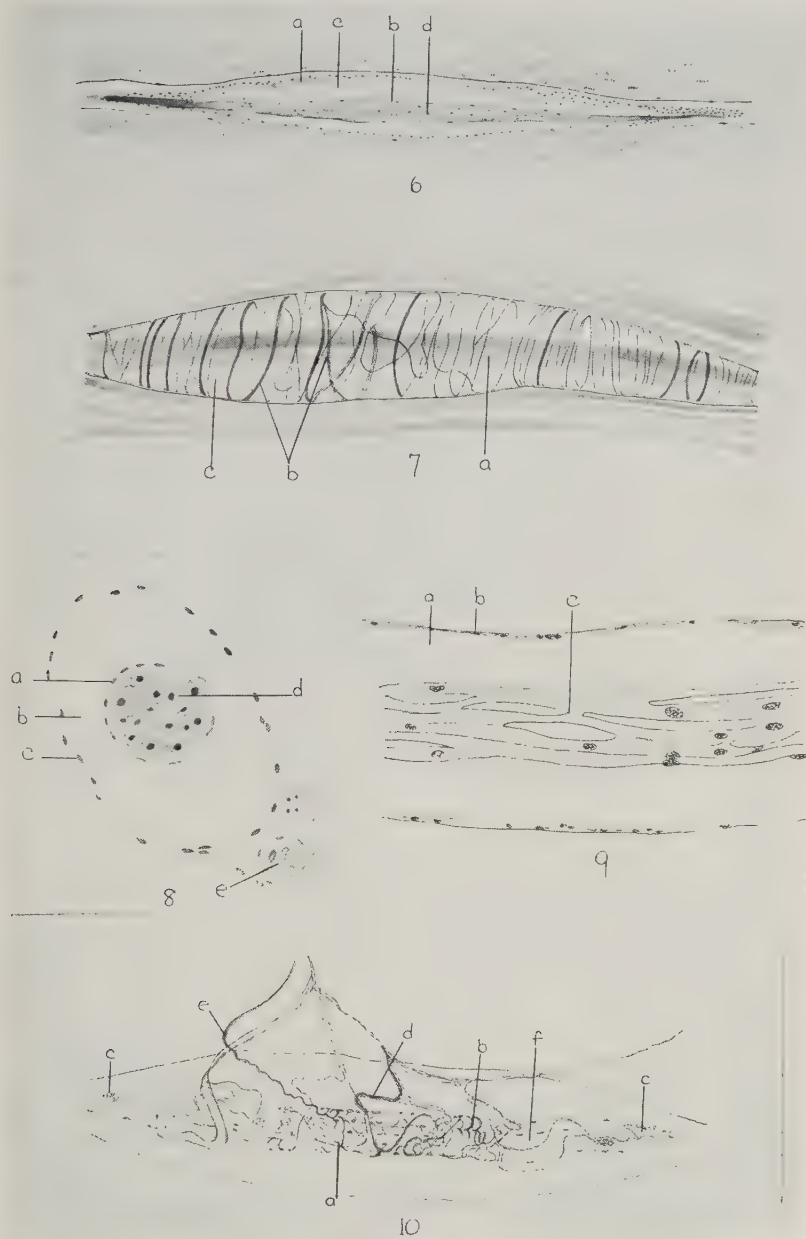


FIG. 77

4 mm. There is no definite relation between length of spindle and that of muscle as suggested by Forster and Batten. Short spindles may be found in long muscles and the reverse is true. Spindles of varying length are often found in the same muscle (Cilimbaris, Tello). The measurements of several investigators are given in table IV.

A neuro-muscular spindle consists of a bundle of slender muscle fibers (the intrafusal fibers or bundle of Weissmann) enclosed within a lamellated capsule, and supplied by several nerve fibers which arborize in an exceedingly complicated manner. Each spindle has its own blood and lymph supply. Morphologically there are simple and compound spindles. The former are usually fusiform, thicker in the center and tapering toward the ends. The compound spindles show a number of dilations, but also become pointed at the ends. In these the number of contained muscle fibers and entering nerves is proportionately increased.

The capsule

Each spindle is surrounded by a capsule consisting of concentric lamellae similar to those of the Pacinian bodies (figs. 76, 5, 77, 6-9). The capsule is in turn surrounded by perimyseal connective tissue which separates the spindle from the ordinary muscle fibers. The number of lamellae varies in different spindles and in different portions of the same spindle. At the widest part there are eight to twelve layers, the number of lamellae decreasing toward each end where they ultimately pass into the perimyseal connective tissue or muscle sheath. The lamellae are extremely thin and are composed of closely packed delicate collagenous fibers disposed both circularly and longitudinally. They are lined on both surfaces by flattened connective tissue cells arranged as endothelial membranes, and according to Ruffini, the cleftlike spaces between the lamellae are filled with lymph. Elastic fibers are also present and their distribution has been worked out by Cilimbaris who distinguishes three types:—longitudinal fibers, most numerous in the inner lamellae, sparser towards the outside; oblique fibers which pass through a number of lamellae, often perforating the whole capsule and continuing in a backward direction; spiral fibers, which are the thickest and most numerous and wind in close spirals from one spindle end to the other (fig. 77, 7).

Between the intrafusal muscle fibers and the innermost lamellae

of the capsule, there is a space which occupies the middle third or more of the spindle (figs. 77, 6-9). This is the lymph space or periaxial space (Sherrington). Here the intrafusal muscle fibers are invested with a delicate capsule, the inner capsule, which like the outer is composed of cells and delicate collagenous and elastic fibrils which are however few in number. The cells send out wing-like processes which traverse the periaxial space and fuse with the innermost cells of the outer capsule. In this manner a system of delicate septa is formed, which permeates the whole lymph space.

The lymph space is filled with an albuminous fluid in which lymphocytes are occasionally seen. That it is truly a lymphatic space has been demonstrated by Sherrington, who was able to inject it through the lymphatics of the leg. Lymphatic vessels running along the course of the muscle fibers have also been described.

The spindle is supplied by blood vessels which course in the perimysium immediately investing the capsule. Most frequently the vessels enter the spindle with the main nerve, but they may enter at the other points as well (Batten). According to Sherrington, one vessel usually runs along the outer portion of the capsule, and gives off capillaries which enter and wind spirally within the spindle.

The intrafusal muscle fibers (figs. 76, 4, and 5; 77, 6-10)

The center of the spindle is occupied by a bundle of muscle fibers, the bundle of Weissmann, so named after its discoverer. The number of fibers entering the spindle fluctuates considerably, but there are always more fibers in the center than at either pole. The recorded numbers are 3 to 10 in man (Koelliker), 3 to 4 in the rabbit (Ruffini), 2 to 12 in cat and monkey (Sherrington), 3 to 15 in the sheep (Cilimbaris). In the compound spindles the number is proportionately increased. Thus Sherrington found over twenty in a double-bellied spindle, and Cilimbaris finds that the normal number may be tripled or even quadrupled.

The muscle fibers show a definite cross-striation which is coarser than in ordinary muscle fibers, and though varying in diameter even in the same spindle, they are always considerably thinner than ordinary fibers. Their diameter in adult man is about 20 micra as contrasted with 60 micra in ordinary muscle (Batten). In the rabbit they measure 19 to 22 micra (Koelliker), in cat and monkey 6 to 28

micra (Sherrington). They are as a rule richer in sarcoplasm but even among the spindle fibers, red and white ones may be distinguished (Cilimbaris). The nuclei are typically central, though near the poles they may occasionally be placed peripherally.

The spindle fibers show, however, two unique features. The parent fibers entering the spindle at one pole, divide dichotomously, the branches anastomosing and forming a network similar to that of heart muscle (fig. 77, 9). This explains the variation in number of muscle fibers at different portions of the spindle, and the great fluctuation in the thickness of the individual fibers. Towards the other pole the network becomes again organized into parent fibers which however, may not be of the same number as the entering ones.

Secondly, each muscle fiber contains in its course a mass of closely packed bubble-like structures which always lie in the spindle belly, though not necessarily in the equatorial position (fig. 76, 4). When examined carefully (Cilimbaris) they appear as aggregations of translucent, pale staining, spherical bodies arranged in the form of a spindle with blunted ends. The spheres vary in diameter from 5 to 15 micra. In a cross-section of the center, three or five bubbles may be seen, the number decreasing toward the poles, but the spheres becoming larger. Hence the poles are only slightly thinner than the middle. At each pole the little spheres become continuous with the muscle nuclei which are at first closely packed, but which gradually become separated and assume their normal distribution. Where the bubble mass is found, the striations are absent and the contractile substance reduced to delicate sarcoplasmic envelopes investing the spheres. Beyond each pole the normal cross-striations reappear.

These translucent bodies have been found and described by numerous investigators, notably Koelliker, Kuehne, Felix, Huber, Batten, Dogiel and Cilimbaris. They are not mentioned by Ruffini who in his careful drawings of the nerve endings in the spindles of the cat, shows cross-striations throughout the whole extent of the muscle fibers.

The special bodies are apparently formed from muscle nuclei which proliferate anatomically, lose their chromatin and undergo hydropic swelling. Cilimbaris working on the eye muscles of the sheep, was able to find at the poles of the bubble masses, forms undoubtedly transitional between them and normal nuclei.

The nerves of the spindle

The spindle is abundantly supplied with nerve fibers of which there are at least two and often many more, the number depending on the length of the spindle. The mode of entrance is variable, the nerve trunks entering both at the equator or near the poles. Most commonly a larger trunk enters the belly, with a smaller one entering near one of the poles. The large majority of the fibers are myelinated and of varying diameter: thick, medium and thin. Besides these there are also present fine unmyelinated fibers which in part at least, are vasomotor in function, and supply the blood vessels of the spindle. The entering nerve trunks have a sheath of Henle, similar in structure to that of the spindle capsule. On reaching the spindle the sheath of Henle becomes directly continuous with the capsule lamellae. The nerve fibers after penetrating the spindle, may at first course spirally, and ultimately yield the arborizations to be described below.

Each spindle is always supplied with both sensory and motor endings which are spatially separated. The motor and sensory fibers may enter in the same trunk or in separate ones. Very often there is a single motor fiber and a trunk of mixed fibers. Sometimes a single motor fiber divides, one branch going to the spindle, the other to ordinary muscle fibers outside. The sensory endings are as a rule supplied by thick fibers, the motor, by thin ones. Occasionally, however, the motor fibers may be thick and the sensory thin (Cilimbaris).

a. Sensory endings. Two types of sensory endings have been described. In one, the usually thick nerve fiber after losing its sheath of Henle and penetrating into the spindle, divides dichotomously into secondary branches which in turn may branch again. These then become closely applied to the muscle fiber, lose their myelin sheath, and at once break up into an extensive flower or ivy-like arborization (figs. 76, 4 and 5, 77, 10, 78, 12) consisting of varicosities connected by fine filaments. The varicosities differ considerably in shape and size, being round, oval, triangular, club-shaped, forked or leaf-like, and the whole arborization is spread out in that portion of the muscle fiber where the translucent bubble masses are found. This is the "secondary" or flower-spray ending described by Ruffini in the spindles of the cat.

Another thick fiber, entering in the same or another nerve trunk,

divides into secondary branches even before reaching the spindle, the branches running together and plunging in the same spindle. Here they divide again, the branches losing their myelin sheath when they become applied to the muscle fibers. Each amyelinate fiber then becomes flattened like a ribbon, and either winds spirally around the muscle fiber, terminating in a free expansion; or the ribbon, varying in width from point to point, runs along one side of the muscle fiber and gives off at intervals terminal branches or bands which like tendrils, clasp the entire circumference of the muscle fiber. This is the primary or annulo-spiral ending of Ruffini (figs. 76, 5, 78, 11).

In the spindles of man, sheep and other forms, such perfect annulo-spiral endings have not been demonstrated, but arborizations similar in arrangement are present. Here the ultimate fibers likewise have a general longitudinal distribution, and give off at intervals branchlets which enclose the muscle fibers in a claw-like manner (figs. 76, 4, 77, 10). The annulo-spiral ending may terminate in portions of the spindle where normal striations are found (fig. 76, 4).

From his studies on the spindles of the cat, Ruffini concludes that the sensory endings represent two distinct types, and are always derived from different nerve fibers. The annulo-spiral is the primary ending, present in all spindles; the flower-like is the secondary ending which may or may not be present. The result of Tello's work would lead to the opposite interpretation. In man and many other mammals, the annulo-spiral forms are not characteristic and may be

FIG. 78

11. Portion of muscle spindle from eye muscle of ox, showing annulo-spiral ending (Ruffini).

12. Portion of muscle spindle from eye muscle of ox, showing flower-like ending (Ruffini).

13. Neuro-tendinous organ from eye muscle of ox (Ciaccio). *a*, entering nerve fibers; *b*, capsule; *c*, tendon fascicles containing terminal arborization.

14. Portion of neuro-tendinous organ from eye muscle of ox, showing terminal branching and characteristic, leaf-like expansions (Dogiel). *a*, capsule; *b*, primary tendon bundle; *c*, nucleus of tendon cell; *d*, fiber furnishing arborization of lower half.

15. Compound neuro-tendinous organ from fascia of back muscle of white rat (Huber and deWitt).

16. Cross section of neuro-tendinous organ of rabbit (Huber and deWitt). *a*, capsule; *b*, tendon fascicles of spindle showing some of the sensory endings; *c*, surrounding connective tissue; *d*, muscle fiber; *e*, entering nerve fiber.



11



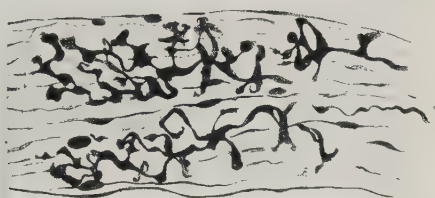
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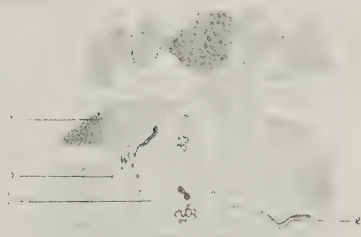
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15



14



10

FIG. 78

absent, while the ivy-like ending is always present, and in man shows a truly remarkable complexity and extent. Developmentally it appears first and stimulates the formation of the bubble mass to which it is always related. The claw-like or annulo-spiral ending appears later and may end in a portion of the muscle in which cross-striations are already formed. It is probable that the difference in the ending is merely one of degree of complication, determined perhaps by local conditions and time of appearance. Forms intermediate in structure have been observed by Ruffini, Dogiel, Cilimbaris, Tello, and others. Indeed Dogiel states definitely that both types are often derived from a single fiber.

b. Plate endings (figs. 76, 5, 77, 10). Each spindle receives one or more motor nerves which terminate in end plates. The simple spindles have one to three, in larger and compound ones the number may reach fifteen or more (Cilimbaris, Dogiel). The number of plates is proportional to that of the muscle fibers.

The fibers branch repeatedly while still in the nerve trunk, the branches ultimately penetrating the spindle. Here some lose their myelin sheath, while others still retain them. The further course varies in different spindles. The fibers may go directly to one pole, or may divide into several branches which lose their myelin sheath, if they have not lost them before, and go to both poles. Here each fiber gives off two or three branchlets each of which terminates in a plate ending. The plates are antler-like arborizations consisting of fine threads beset with varicosities and cross pieces of various form. Some of the plates are smaller than ordinary motor plates, some are of the same size. Others may be so extensive as to enclose the whole periphery of the muscle fiber. Occasionally such large plates represent the fused endings of two separate nerve fibers. Not infrequently a single muscle fiber may receive several plates.

The location of the motor apparatus is usually near one or both poles of the spindle. More rarely they may be found between two sensory arborizations, as in some of the compound spindles. They are, however, always spatially distinct from the sensory endings, and never terminate where the bubble-shaped structures occur.

There has been considerable dispute regarding the significance of the plate ending. Ruffini, basing his opinion on the histological pictures, considers them a type of sensory ending, and this belief is shared by Sherrington, Giacomini, and a few others. However, a

wealth of histological, experimental and embryological data bears witness that they are true motor plates, as first suggested by Kerschner and Cajal, and this view is held by Onanoff, Weiss and Dutil, Cipollone, Huber and deWitt, Dogiel, Perroncito, Cilimbaris and Tello. Onanoff and Cipollone have shown that the plates degenerated with section of the motor fibers, but remained intact in sensory degeneration. Their structure is similar to ordinary motor plates, and they contain the characteristic granular substance found in the latter (Dogiel). Again, a single motor fiber may divide one branch furnishing plates for the muscle fibers of the spindle, the other supplying ordinary muscle fibers. And more recently Tello has shown that these endings develop simultaneously with the rest of the motor plates, a considerable time after the intricate sensory endings have been fully established.

c. Other nerve fibers. Besides the myelinated fibers a number of fine unmyelinated fibers are found in each spindle. Some are vasomotor fibers which wind spirally around the spindle and supply the fusar blood vessels (fig. 76, 4). The significance of other exceedingly fine fibers, which often end in little club-shaped thickenings, is not fully understood.

Physiological considerations

The neuro-muscular spindles are sense organs stimulated by the contraction of the intrafusal muscle fibers. They function as isotonic dynamometers (Luciani), equipped mechanically for the perfect registration of even the faintest change in the form of the muscle fibers. The network of muscle fibers permits a spreading of the contraction wave over a larger area, and furnishes an enormous surface for intimate and extensive contact with the rich sensory arborization. The bubble apparatus may be considered an accessory structure for still greater refinement of the delicate receptivity suggested by the elaborate nerve endings. With each contraction there would occur a displacement and pressing together of spheres, and these by their movement and elastic rebound, would intensify the stimulation of the sensory endings (Cilimbaris).

The neuro-tendinous organs

In 1880, Golgi described in detail a type of sensory ending which he found in the tendons of the frog, lizard, bird, cat, dog, rabbit, and

man, and to which he gave the name of nervous musculo-tendinous end organs (*organi nervosi terminali musculo-tendinei*). These endings, now called the neuro-tendinous organs or spindles, have since been found in practically all vertebrates as characteristic sensory structures associated with the tendons, aponeuroses and intermuscular speta. In man and other mammals they are very numerous and in spite of considerable individual variation in form and complexity, they all exhibit a fundamental similarity in the nature of their terminal arborization. The relation of these nerve endings to the tendon fascicles which they innervate, may be compared with that of the neuro-muscular endings to the intrafusal muscle fibers.

Besides the neuro-tendinous spindles a varied number of other sensory structures are found in the same regions, often in close relation with the spindles. They include the Pacinian bodies, the corpuscles of Krause and of Golgi-Mazzoni, and similar encapsulated forms. These have not been included in the discussion, since they are not characteristic of the locomotor system, but have a wide distribution in other portions of the body where they subserve other than proprioceptive functions. The account is therefore limited to those structures specifically known as neuro-tendinous organs.

As early as 1875, Sachs studied the nerve endings in the tendons of some amphibia, birds, and mammals. In the frog and salamander especially, he succeeded in impregnating what he believed to be the terminal arborization. He states that the terminal myelinated fibers break up into a confused mass of unmyelinated branchlets which then spread mould-like in all directions. He believes them to be sensory organs. Rollet (1876) likewise reports a plexus of medullated nerve fibers in the tendon of the sterno-radialis muscle of the frog. He states that the plexus terminates in expansions whose structure is similar to that of motor plates.

The first comprehensive account of the structure and distribution of these organs was given by Golgi (1880) who studied the endings in the tendons of man, dog, cat, rabbit, bird, lizard, and frog. The organ is spindle-shaped and situated at the junction of muscle and tendon. One end is always attached to the muscle, the other becomes continuous with the tendon fascicles, hence the name of musculo-tendinous end organs. They are found in all the muscles, except the eye muscles. In birds and mammals they have a definite capsule which is lacking in the frog and lizard. He gives a detailed account

of the terminal endings in the various forms and points out their general similarity. In the following year Marchi demonstrated the presence of the spindles in the extrinsic eye muscles of man, cattle, pig, dog, cat, and rabbit, but added little to the data given by Golgi.

Since the fundamental work of Golgi, our knowledge regarding the distribution, structural variation and details of end arborization of these organs was materially extended by the investigations of Cattaneo (1887), Kerschner (1888), Pansini (1888), Ciaccio (1889-1891), Ruffini (1893), Smirnow (1893), Sherrington (1894), Giacomini (1898), Huber and deWitt (1900), and Dogiel (1902-1906). Especially important and comprehensive are those of Cattaneo, Ciaccio, Huber and deWitt, and Dogiel.

TABLE V
VARIATIONS IN DIMENSIONS OF SPINDLES

AUTHOR	LENGTH	WIDTH	ANIMAL
	<i>mm.</i>	<i>mm.</i>	
Golgi.....	0.3-0.8	0.08-0.12	Several mammals
Koelliker.....	1.28-1.42	0.17-0.25	Man
Koelliker.....	0.24-0.79	0.02-0.11	Rabbit
Cattaneo.....	0.08-0.8	0.05-0.4	Several mammals

The sensory function of these organs was experimentally demonstrated by Cattaneo in 1888. He cut the posterior roots but found no degeneration of the spindle nerves, though a definite ataxia resulted. On cutting the anterior root the motor nerves to the muscles degenerated, but the spindles again remained normal. He then sectioned the sciatic nerve with resulting spindle degeneration. He concluded that the spindle nerves were of ganglionic origin, and subserved muscular sense. It may be noted that Brazzola (1890) found degenerative changes in the spindles in several cases of tabes dorsalis.

Structure and distribution. The neuro-tendinous organs (figs. 78, 13, 78, 15, 79, 21 and 22) are found in practically all vertebrates, including the fishes (Pansini). They consist of several tendon fascicles, supplied by one or more myelinated nerve fibers which end in a characteristic terminal arborization. A lamellated connective tissue sheath is almost always present in mammals and birds, usually absent in reptiles, and always lacking in amphibia and fishes. Each spindle has an independent blood supply, but lymphatics have not been demonstrated.

In mammals the spindles are usually fusiform, but elongated cylindrical forms are not uncommon. These also taper slightly at ends. Compound spindles have been observed by Ciaccio, Huber and deWitt and others (fig. 78, 15).

The size of the spindles varies considerably, but only few careful measurements have been reported. Some of the recorded dimensions are given in table V. Ciaccio records a human tendon organ nearly 3 mm. long and 1.5 mm. wide. The spindles are smaller and simpler in the young, larger and more complex in the adult (Cattaneo, Huber and deWitt). According to Cattaneo the dimensions are also proportional to the size of the animal, being, for instance, larger in the dog than in the guinea-pig, still larger and more complicated in man.

The spindles are found in practically all muscles, including the extrinsic muscles of the eyes (Marchi, Ciaccio, Huber and deWitt, Dogiel). They are apparently more numerous in the lower than in the upper extremity. They are especially abundant in the large fascia of the back muscles, the tendons of the gastrocnemius, tibialis posticus and extensor longus digitorum of the cat, and in those of the interossei of the foot of the rabbit (Huber). Dogiel found them in great numbers in the eye muscles of cattle.

The position of the spindles is typically at the junction of tendon and muscle, one end being attached to the muscle, the other continuous with the tendon fascicles. In a number of instances, however, they are tendinous at both ends (Huber and deWitt, Dogiel, Ciaccio). In some muscles, the spindles are not situated in the tendons proper, but in the muscular septa or sheaths. This Dogiel finds, is the most common position in the muscles of the anterior body wall of the rabbit. The spindles lie in the septa between the ends of the muscle fibers, only rarely extending with one extremity into the main tendon. Even less frequent is the complete inclusion of the spindle within the tendon.

The tendon fascicles of the neuro-tendinous organs have a general embryonal appearance, possessing more nuclei and staining more deeply than the ordinary tendon fascicles.

In the mammals the spindles are usually enclosed within a lamellated capsule resembling the sheath of Henle of a nerve fiber (figs. 78, 13, 14 and 16), but the thickness is extremely variable. Some spindles have only a single layer of connective tissue fibers with a few nuclei, and the capsules are easily torn off during preparation.

The more characteristic, thicker capsules consists of a number of layers of collagenous fibers between which there are flattened cells. The outer surface of the sheath is covered by an endothelial membrane. No elastic fibers have been demonstrated.

While Golgi, Huber and others have found a capsule in all mammalian spindles described by them, non-encapsulated forms have been observed by several investigators. Ciaccio states that in the bat the spindles of the posterior extremities possess sheaths, but that capsules are lacking in those of the anterior extremities, and he concludes that the capsule is not a constant feature of the mammalian spindle. Dogiel studied the spindles in the tendon of the transversus, and in the tendinous inscriptions of the rectus muscle of the rabbit. Here practically all are non-encapsulated, and are placed not in the tendon proper, but in the intermuscular septa near the ends of the muscle fibers.

The blood supply of the spindle comes from the vessels of the surrounding connective tissue. Each spindle usually receives two blood vessels which run on either side, and at intervals give off side branches which anastomose with those of the other side and form a long-meshed plexus resembling that of muscle tissue (Cattaneo).

The neuro-tendinous spindles are typically supplied by a single thick nerve fiber possessing unusually short internodal segments. Occasionally two or three independent fibers may innervate the organ. The fiber often divides into two or three fibers which run in the nerve trunks of the intermuscular septa. On reaching the spindle these plunge into the organ, losing their sheath of Henle which becomes continuous with the capsule. The fibers always approach from the muscular side, and most commonly penetrate the spindle at the center. Less frequently the fibers enter at the muscular pole.

Within the spindle the fibers divide into primary, secondary and tertiary branches which still retain their myelian sheaths. The tertiary fibers then split into numerous non-myelinated branches which wind between and around the primary tendon bundles, meanwhile giving off side branchlets which themselves repeatedly divide (figs. 78, 13 and 14, 79, 22). All these terminal branches have the appearance of delicate ribbons which along their course, and especially at the points of branching, exhibit large, flat polyangular, leaf-like expansions or plates (fig. 78, 14). Delicate filaments, extending from the ends of the expansions, connect the plates with each other

and with those of neighboring branches. According to Dogiel, the terminal branches and plates form an enveloping net work around the primary tendon bundles. The flat expansions (granular masses) which are characteristic of the neurotendinous terminations, consist of neurofibrils and perifibrillar substance (Dogiel).

While all the spindles show the characteristic endings described above, there is considerable individual variation in the architecture and complexity of the whole apparatus. These variations are conditioned by the number and position of the entering nerves, the number and length of the non-myelinated branches and the number and size of the granular expansions. In the mammal Huber and deWitt recognize four main architectural types.

In some spindles, the nerve entering at the center divides into two primary branches which go to the extremities of the spindle. The internodal segments become progressively shorter, and break up near the poles into secondary and tertiary branches which form the end arborizations. A few side branches are given off by the primary fibers, which at once divide, lose their myelin sheath and arborize. Such spindles have a massive ramification at the poles, with few fibers in the center (fig. 78, 15). They are frequently seen in most mammals and are quite numerous in the cat.

More typically, the fiber entering at the center divides into two, the branches going toward the poles. But these branches are short,

FIG. 79

17. Nerve fibers destined for the neuro-tendinous organ in leg muscle of chick embryo of nine days' incubation (after Tello). *a*, embryonal tendon; *b*, muscle fibers; *c*, interfascicular connective tissue; *d*, fiber which is forming neuro-tendinous endings.

18. Zone of junction between tendon and muscle in chick embryo of twelve days' incubation (after Tello). Thickened end (*e*) of nerve fiber splits into numerous branches terminating in small rings. Other letters as in figure 79, 17.

19. Early neuro-tendinous spindle in chick embryo of twelve days' (after Tello). Lettering as in figures 79, 17, and 79, 18.

20. Developing neuro-tendinous spindle in chick embryo, after fifteen days' incubation (after Tello). Lettering same as in figure 79, 17.

21. Neuro-tendinous spindle in human foetus of six months' (after Tello). *a*, ends of muscle fibers; *b*, nerve fiber supplying spindle and forming the terminal ramification; *c*, tendon of spindle; *d*, ordinary tendon; *e*, tendinous implantation of muscle fiber in ordinary tendon.

22. Neuro-tendinous organ of rabbit (Huber and deWitt).

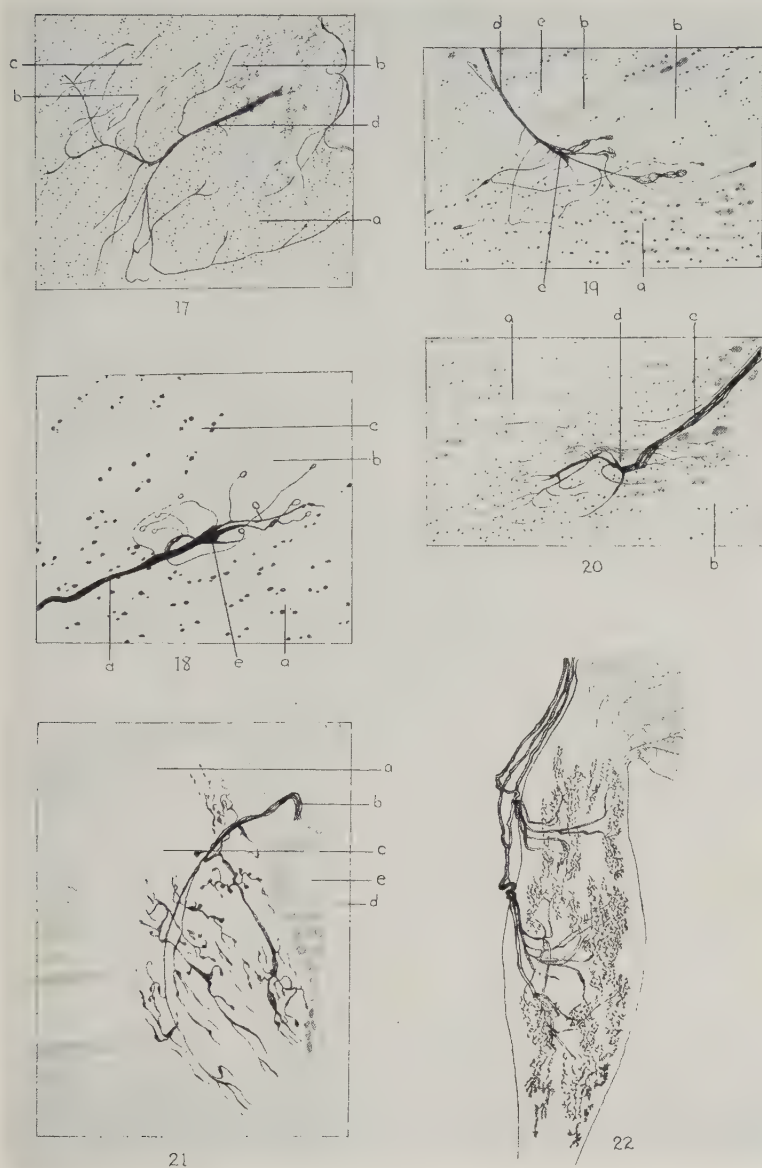


FIG. 79

and split into numerous secondary branches, many of which course back centrally, while others go to the extremities. The secondary fibers then divide and ultimately yield a terminal ramification which is dense in the center and gradually diminishes toward the poles.

In still others the fiber divides into several branches before entering the spindle, or the organ may be supplied by several independent nerve fibers. In either case two or more fibers enter, split into secondary and tertiary branches which form an end arborization resembling that of bushes or trees with short trunks (fig. 79, 22).

Finally, in a small number of spindles, the fiber enters at the muscular extremity, and either itself or its primary branches run for some distance parallel with the long axis of the spindle, giving off side branches at intervals. The main fibers as well as the side branches then break up into an end ramification, the whole spindle resembling a tall branching tree (Huber and deWitt).

The Pacinian corpuscles

The Pacinian corpuscles were discovered by Vater (1741), but the first account of their structure was given by Pacini (1842). In the locomotor system they were observed in the joints by Cruveilhier (1834) who believed them to be pathological structures. Since then they were studied by Henle and Koelliker (1884), Herbst (1848), Krause (1861), and especially by Rauber (1865-1867) who gave a comprehensive account of their structure and detailed distribution in the body. Additional data were given by Ruffini, Sherrington, Key, Retzius, Schaefer, and others.

The corpuscles have a remarkably wide distribution in the body, being found almost anywhere, but especially numerous in the subcutaneous tissue of the volar surface of the fingers, hands, toes, and feet; in the external genitalia, and in the mesenteries.

Nowhere, however, are they more numerous than in the arthroperiosteal system, where their distribution has been carefully studied by Rauber. Though most numerous in the fibrous capsules of the joints, they are likewise abundant in the periosteum, ligaments, muscular septa and sheaths, and in many tendons. In these regions they must undoubtedly be considered as organs of proprioceptive function.

The Pacinian bodies (fig. 80, 27-30) are stalked, ovoid or pear-shaped bodies, consisting of a nerve fiber surrounded by an inner

core or bulb which in turn is enclosed within a lamellated capsule. Forked bodies are not infrequently seen. The entering nerve fiber with its perineurial sheath (sheath of Henle) constitutes the stalk, the perineurial lamina becoming continuous with the capsular lamellae. The larger corpuscles are 2 to 3 mm. long and 1 to 2 mm. thick, the smallest have a length of 2 to 8 mm. (Raubert).

The number of the capsular lamellae varies enormously. The small corpuscles found in many tendons (Ruffini) have only four to eight layers (fig. 80, 30), in the larger corpuscles there may be as many as sixty (fig. 80, 28). Each lamella consists of a layer of collagenous fibers which are loosely arranged, and disposed both circularly and longitudinally. On each surface the layer is covered by an endothelial membrane (fig. 80, 31) which becomes continuous with the flattened cells of the perineurial sheath (sheath of Henle). Elastic fibers are likewise present, and run in all directions, traversing the thickness of the lamellae from one surface to the other. Between the lamellae are the cleft-like intercapsular spaces filled with lymph (fig. 80, 31). The lamellae themselves contain a similar fluid occupying the spaces between the fibers, and appear swollen and translucent. The corpuscular lymph may be emptied by puncture, when the lamellae assume the shrunken appearance characteristic of most preparations (figs. 80, 27 and 80, 28).

The lamellae immediately surrounding the inner bulb are closely packed and appear to form a system of their own. The outer ones are more loosely arranged and have correspondingly wider intercapsular clefts. The whole corpuscle is surrounded by loose connective tissue.

The core or inner bulb, enclosing the elongated nerve termination, extends vertically through the corpuscle. It consists of a granular, albuminous substance, which appears striated in the outer zone and is lined by a peripheral row of elongated nuclei. The core is apparently formed in part from the neurolemma, in part from the perineurial connective tissue (Raubert).

The nerve fiber entering at the stalk, passes straight to the core, the lamina of its perineurial sheath becoming continuous with the outer lamellae of the capsule. Since the capsular layers far outnumber those of the sheath of Henle, only a number show such continuity, the remaining lamellae ending with rounded margins against the delicate connective tissue or sheath of Schwann which encloses the

perforating nerve fiber. On reaching the core the fiber loses its myelin sheath, and the naked axis cylinder traverses the length of the inner bulb, when it may end in a single terminal thickening. More usually it shows a number of neurofibrillar varicosities beyond which it constricts and ultimately terminates in one or more button-like thickenings (fig. 80, 27). Each of the terminal buttons, or a group of them, are always surrounded by bay-like extensions of the inner core.

The Pacinian corpuscles of the locomotor apparatus, though conforming to the structure described above, show considerable variation as to size, number of capsular lamellae, and mode of nerve termination. An especially modified form is found in many tendons and has been described by Ruffini and others. These corpuscles are as a rule small, very elongated and often forked (fig. 80, 30). The capsule has only four to eight lamellae, the inner core is massive, and the axial nerve fiber correspondingly thick. Ruffini believes that they have a definite relation to the tendon spindles with which he finds them always associated. In the cat, the fiber which supplies the Pacinian body, pierces the capsule of the tendon organ and runs for some distance

FIG. 80

23. Section through membrana interossea tibia-peronaea of chick, twelve days' incubation (after Tello). *a*, terminal fiber destined for Pacinian corpuscle; *b*, forking fiber; *c*, embryonal connective tissue.

24. Pacinian corpuscles of thirteen days' chick embryo (after Tello): *a*, terminal nerve fiber; *b*, condensation of connective tissue cells.

25. Pacinian corpuscles from interosseous membrane of fifteen-day chick embryo (after Tello). *a*, terminal nerve fiber; *b*, innerbulb; *c*, lamella of capsule.

26. Pacinian corpuscles from interosseous membrane of chick after fifteen days' incubation (after Tello). *a*, terminal nerve fiber; *b*, inner bulb; *c*, capsular lamellae.

27. Pacinian corpuscle from mesentery of cat (after Ranvier). *a*, outer lamellae; *b*, inner lamellae; *c*, inner bulb; *d*, axial nerve fiber; *e*, terminal varicosities; *g*, entering nerve fiber with sheath of Henle.

28. Transverse section of Pacinian corpuscle. *a*, outer lamellae; *b*, inner lamellae; *c*, inner bulb enclosing axial nerve fiber.

29. Pacinian corpuscle from mesentery of cat, showing endothelial membrane of outermost lamella (after Schaefer).

30. Pacinian corpuscle from tendon (after Ruffini). *a*, capsule; *b*, inner bulb, *c*, axial nerve fiber.

31. Schematic drawing of two lamellae of a Pacinian corpuscle in transverse section. *a*, endothelial membrane; *b*, interlamellar cleft.

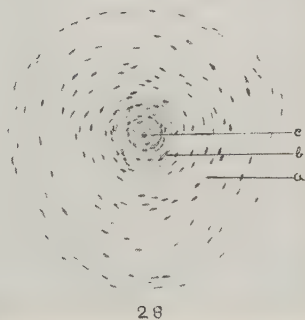
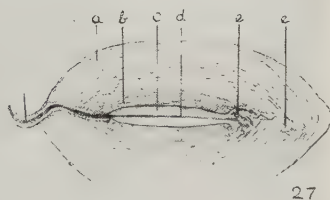
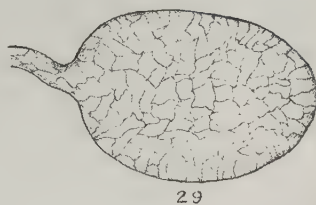
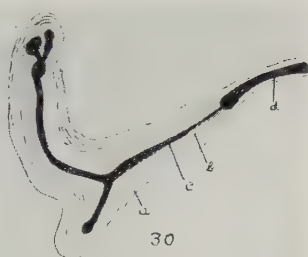
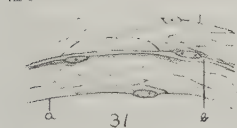
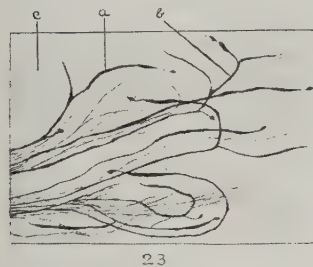
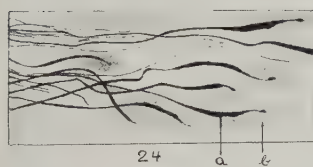
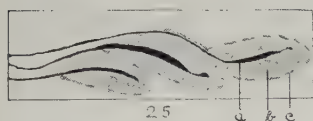
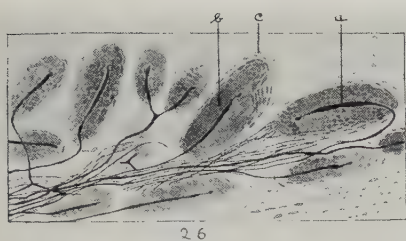


FIG. 80

beneath the surface. It then re-pierces the sheath in an outward direction, wholly or in part, and ends in its own small Pacinian corpuscle. This corpuscle lies in the outermost fascia of the tendon organ, often in a little hollow, scooped out of the surface of the organ. In the rabbit the corpuscles also lie near the tendon spindles but are not integrated with the connective tissue of the latter (Ruffini).

According to Cattaneo and others the juxtaposition of the tendon spindles and Pacinian bodies is accidental, and the two are always anatomically distinct, and receive independent innervation. In many cases Pacinian corpuscles are not present in the close vicinity of the tendon organs.

Other encapsulated receptors such as the corpuscles of Ruffini and of Golgi-Mazzoni, are likewise found scattered in the connective tissue of the locomotor system. They have however, a wide distribution in the body, and compared to the proprioceptors already described they play only a minor rôle in kinesthetic sensibility. Their consideration would entail a discussion of the various types of cutaneous and more deeply placed sense organs, which is obviously beyond the scope of this survey.

THE DEVELOPMENT OF THE PROPRIOCEPTIVE ORGANS

In the rich literature on the proprioceptors, there are a few instances which give accounts of foetal spindles or those of infants. In man, Koelliker described the spindle of a two-months' foetus, and Christomanos and Stroessner made a comparative study of the spindles in the human foetus, new-born, infant and adult. But in these as well as other cases, no information is given as to their mode of formation. The observations of Weiss and Dutil (1895) on the guinea-pig are vague and fragmentary, and even less adequate are those of London and Pesker (1906). Practically nothing was known about the embryology of the proprioceptors, until Tello's work appeared (1917), giving an almost complete account of the development of all the three types of sense organs found in the locomotor apparatus. Extending over a period of years, this thorough work includes investigations on the rabbit, cat, dog and man, with especially complete data on the chick. In man about twenty fetuses and children were studied. The following is practically a condensed account of Tello's work.

In the chick, on the fifth day of incubation, fibers separate from the mixed nerve trunks which constitute the spinal nerves, and arrive

at the border of the myoblast masses which form the anlage of the embryonic muscle. On the sixth day the fibers begin to penetrate into the muscle and as in other cases, exploratory fibers are first sent out (pathfinders, Harrison), which act as guides for the others. On the seventh day the penetration is considerable and extensive branching has taken place, the extent varying in different muscles. It is comparatively simple in the muscles of the trunk and limbs, more pronounced in the face muscles, and most elaborate in the muscles of the tongue where a complex net-work is formed. The nerve fibers always penetrate the muscle perpendicular to the long axis of the myoblasts which now have become multinucleated cylindrical fibers. Exploratory fibers move freely between the connective tissue cells, their end bulbs leaning against the muscle fibers. Occasionally some accompany the muscle fibers before resuming their transverse course.

As the myoblasts increase in number and differentiate, there is simultaneous branching and differentiation of the nerve fibers. And when the total number of muscle fibers is reached (fourteen to fifteen days), increase of the nerve branching ceases, and the last formed branches come in contact with the individual muscle fibers. From this time on, further growth is shown only in the thickening of the axis cylinder, the appearance of myelin, the modelling of the end arborization, and the organization of the connective tissue elements, just as the muscle fibers undergo hypertrophy without further formation of new fibers.

During the first few days of intra-muscular branching, no difference can be observed with regard to the thickness of the various nerve fibers, nor is there any indication as to their ultimate place of innervation. But from the ninth day on, the sensory nerves appear considerably thicker and stand out in contrast to the thinner motor nerves. On the ninth day the fibers destined for the neuro-tendinous organs, can be easily distinguished by their thickness and course. Those for the neuro-muscular spindles appear between the tenth and eleventh day. This difference in thickness between sensory and motor fibers is very conspicuous, especially since no such difference can be observed in the large mixed nerve trunks. It is probably explained by the fact that the motor fibers, destined to innervate a number of muscle fibers, split repeatedly, the branches becoming progressively thinner as the area of innervation is reached. On the other hand, the sensory fibers which ultimately innervate only a few muscle fibers,

divide but little if at all, and hence retain their original diameter up to the point of terminal branching. While this difference is partially eliminated by the subsequent hypertrophy of the muscle cells and motor fibers, it is still definitely recognizable in the adult.

The neuro-muscular spindles (fig. 76, 1-4)

Beginning formation of neuro-muscular spindles may be observed in the chick on or about the eleventh day of incubation. Certain thick exploratory fibers from the intra-muscular nerve trunks approach a bundle of myoblasts which are in their most intensive period of proliferation, and run along the embryonal muscle fibers, giving off varicosities along their whole course (fig. 76, 1). These nerve fibers and the bundle of myoblasts are destined to form the adult spindle. It is of course possible that a single muscle fiber may thus be innervated, and the future spindle consist of but a single fiber, but such conditions are actually very rare.

Before innervation, the primitive myofibers, separated by embryonal connective tissue, are similar in structure, and it is apparently a matter of chance as to which of the muscle bundles will receive the first exploratory fibers. But once the contact is made, the presence of the nerve fiber profoundly influences the further evolution of the innervated myofibers (Weissmann's bundle) and of the connective tissue. It stimulates intensive amitotic proliferation of the muscle nuclei, and inhibits myofibril formation. The nuclear aggregations always occupy a central, though not necessarily equatorial position, and cause an enlargement of that portion of the muscle fiber (fig. 76, 3). These nuclear masses are retained when the ordinary muscle fibers and the polar portions of the spindle fibers have become fully differentiated, the embryonal condition persisting in the adult (fig. 76, 4).

The perifascicular connective tissue becomes hypertrophied, and begins to show organization into a lamellated capsule (fig. 76, 2). On the other hand, the intrafascicular tissue is greatly reduced, so that each muscle fiber does not receive its individual sheath, as is the case in ordinary muscle.

During the proliferative period of the muscle nuclei (eleventh to thirteenth day), the nerve fiber undergoes extensive arborization. As was mentioned above, the thick branchlets which approach the myoblasts give off numerous varicosities along their course (fig. 76, 1).

Occasionally, all fibers which enter the spindle radiate from a single, thick terminal fiber (fig. 76, 2), but in every case the course of the nerves is always paralld with the muscle fibers. On the thirteenth day each primary branch sends out several secondary branches which course perpendicular to the first, and from the beginning tend to curl around the muscle fibers (fig. 76, 3). By the thirteenth day, the the neuro-muscular spindles, though rudimentary, are definitely recognizable as such. The myofibers contain numerous nuclei; lamellae are forming in the connective tissue; and the nerve arborization is beginning to show a spiral or ring-like disposition.

Around the fourteenth day, new, usually thinner fibers penetrate the spindle. These as a rule course up or down and terminate near the poles as little club-shaped expansions, unlike the complicated sensory branching which limits itself to the region of nuclear aggregations. Still finer fibers enter the spindle, and generally take a spiral course (fig. 76, 4).

In the final period of embryonal development the modelling of the spindle is completed with the differentiation of the various sensory endings and the formation of motor plates. All types of nerve fibers can be easily recognized in the large neuro-muscular spindle from a human foetus of six months, shown in figure 76, 4. The thick fiber which enters at *a*, furnishes the elaborate flower or ivy-like ending, *c*, the farthest muscle fiber receiving the richest arborization. This portion of the muscle fibers still contains a large aggregation of nuclei having the appearance of bubbles. The thick fiber at *b* yields the claw-like or annulo-spiral ending *d*, applied to a portion of muscle in which differentiation of myofibrils has taken place. The bundle of thinner motor fibers, *e*, runs toward the pole of the spindle, and sends out exploratory fibers with terminal end-bulbs, *f*. Entering at *a* are the still finer vasomotor fibers, *g*, which wind spirally around the spindle.

It will be noted that the sensory endings are richly unfolded when the motor plates are as yet unformed. In the chick the sensory arborization is present in its ultimate form on the fifteenth day, while motor plate formation does not begin till the eighteenth day. Similar conditions are observed in the cat, dog, rabbit and man, the motor endings appearing at a much later stage, simultaneous with the formation of such endings in ordinary muscle fibers.

The neuro-tendinous organs (fig. 79, 17-21)

The nerves destined for the neuro-tendinous organs can be recognized in the chick from the ninth day on, when several thick fibers leave the intra-muscular nerve trunks, and run directly and without branching to the boundary zone of the muscles where the ends of the muscle fibers are surrounded by numerous connective tissue cells constituting the embryonal tendon. There the parent fiber splits into a number of finer ones which then search out the ends of the muscle fibers (fig. 79, 17). Should the nerve fiber, as is usual, land in a place where a bundle of myoblasts is present, it suddenly splits into a considerable number of fibrils which end in little bulbs or rings, and, establish contact with all the myofibrils of the bundle (fig. 79, 18).

From the twelfth day, the modeling of the tendon organ is determined by the organization of the connective tissue, and at the same time the arborization becomes more complete by the tree-like branching of the nerve fibers. The place of penetration of the parent nerve is characterized by the condensation of connective tissue cells which surround the ends of the myofibrils and separate them from the outer, now fibrous portion of the tendon (fig. 79, 19). At this stage, the end varicosities in contact with the myofibers are large, and new branches are sprouting from both the stem and terminal fibrils (fig. 79, 19). However, only few of these new fibers go to the ends of the myofibers, the majority now spreading into the cellular connective tissue mass (fig. 79, 19). On the fifteenth day the cellular aggregation is so large, that it is hardly possible to distinguish the ends of the myofibers (fig. 79, 20), and from this time on, the relation between the nerve fibers and muscle fibers becomes lost.

Collagenous fibers appear in the cellular mass and increase in the same measure as the ends of the muscle fibers disappear, either through shrinkage or absorption, their place being taken by little tendons (implantation tendons). These implantation tendons are longer and stouter than those of ordinary muscle fibers, as they really serve for the insertion of a myofiber bundle innervated by the spindle (fig. 79, 21).

While originally all myofibers have an equal neurotropic effect on the nerve, once the innervation is made, a new factor is present which definitely influences the further development of the innervated area.

The factor itself is not understood, but its effect is clear, and is expressed in a hyperplasia of the connective tissue, and a delay or absence of muscle fiber differentiation. The hyperplasia leads to the formation of a long and stout tendon serving for the insertion of a myofiber bundle and containing the ultimate sensory ending (fig. 79, 21). The ends of the muscle fibers lack myofibrils from the beginning. And later when the sarcoplasm likewise disappears, the effect is a shortened muscle bundle associated with the spindle (fig. 79, 21). With the progressive hyperplasia of the connective tissue and its transformation into the spindle tendon, there is a corresponding growth in the richness of the nerve branching. At first the branches lie parallel to the tendon fibers (fig. 79, 21). Later the fibers and flattened varicosities wind around the tendon bundles, until the ultimate appearance of the adult spindle is produced.

The Pacinian corpuscles (fig. 80, 23-26)

It must be remembered that the Pacinian corpuscles are not characteristic of the locomotor system alone, but are also found in the skin and in the connective tissue of the various serous membranes and of other structures. In the chick, Tello studied them in the interosseous membrane between tibia and fibula, where they are unusually numerous. Unfortunately this membrane gradually ossifies in the vicinity of the bones with consequent disposition of calcium-salts which are diffusely distributed. As a result, the silver (in Cajal's technique) is precipitated in such masses that a proper interpretation of the histological pictures of the later stages is practically impossible. Hence only the earlier stages are described by Tello.

On the seventh day, the interosseous membrane is invaded by a large number of nerve fibers which spread over its anterior surface. By the ninth day the fibers have become so numerous and crowded, that they form one of the richest ramifications found in the embryo. It is difficult to explain adequately this astounding aggregation of nerve fibers, but it suggests the significant role which these membranes and similar structures play in the development and organization of kinesthetic sensations.

On the tenth day the nerves show a differentiation into thick and thin fibers, most of them ending in little club-shaped expansions. No other differences are observed at this time. The first visible signs of Pacinian corpuscle formation appear on the eleventh or

twelfth day, *i.e.*, at the time when the neuro-muscular and neuro-tendinous organs are beginning to differentiate. The thicker fibers, some coursing in a straight line, others describing wide curves show a longitudinal thickening, but then constrict again and ultimately terminate in a club-shaped expansion (fig. 80, 23). Often the parent fiber will fork and give origin to two longitudinal thickenings (fig. 80, 23).

It will be noted that these early endings are already similar to those of the adult corpuscles, but as yet there is no trace of a capsule, the nerves ending among the cells of the primitive connective tissue. From this time on, further growth is expressed in the progressive hypertrophy of the nerve fiber which retains however, its early form, and in the transformation of the connective tissue into the central granular mass and capsular lamellae. On the thirteenth day the cells immediately investing the terminal thickenings become more closely packed and form a central or periaxial mass, while the rest of the connective tissue cells have the same appearance as before (fig. 80, 24). This periaxial mass becomes more pronounced, as the connective tissue cells around them flatten and organize to form the first lamella of the capsule (fig. 80, 25). In a chick of fifteen days a number of lamellae are already formed, and the pericapsular connective tissue has assumed a fibrous appearance (fig. 80, 26). The periaxial mass retains, however, its embryonal, cellular character.

While later stages have not been described, the probable course of further evolution is indicated by the structures present. The periaxial mass undoubtedly forms the granular substance or inner bulb surrounding the nerve fiber. And as more lamellae are progressively formed from the connective tissue, the adult form is ultimately established.

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CHAPTER VI

THE COMPARATIVE MORPHOLOGY OF THE PROPRIOCEPTORS¹

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THE afferent nerve endings for the reception of stimuli are designated by Sherrington as receptors and these, according to their anatomical location and the origin of the stimulus acting upon them, are classified in three groups. Thus, the exteroceptive terminals are situated principally in the ectoderm and receive stimuli which act on the organism from without; the interoceptive field contains a variety of specialized nerve endings for the reception of stimuli arising within the viscera and internal body surfaces, and the terminals which receive stimulation within special tissues due to the actions of the organism itself are known as proprioceptors, and these are found chiefly in muscles, tendons, joints, and blood vessels.

Although Sherrington states that the proprioceptive endings are different from those in the exteroceptive field, which is rich in a variety and number of receptors, he does not specify the character of the terminals in the respective fields. It is evident, however, that the exteroceptive and proprioceptive areas are in part, at least, contiguous and there is in the subcutaneous tissue an interesting group of nerve endings which, from their anatomical location, might be either exteroceptive or proprioceptive in function. Physiological interdependence of the two fields is also recognized by Sherrington in the statement that the proprioceptors are primarily, in many cases, excited by a receptor of the exteroceptive field, and reflexes in the proprioceptive field are, therefore, "habitually attached and appended to certain reflexes excited by exteroceptive organs."

Not only do the superficial and the deep fields overlap, but each contains free and encapsulated nerve endings; and the free terminals in the epithelial covering often contribute filaments to the corium and subcutaneous tissues while the tactile corpuscles of Meissner,

¹ The illustrations, unless otherwise noted, are copies from Barker, and Renaut and Regaud where full acknowledgment is made.

situated in the mesoblastic layer send occasional axones into the epidermis proper; and, furthermore, certain nerve endings of epiblastic origin, such as Grandry's corpuscles, are found in adult life, in the subepithelial tissue. Thus, it is difficult to make an anatomical distinction between the exteroceptive and proprioceptive fields, or to determine to what depth a nerve terminal must descend before it might properly be regarded as a deep proprioceptor. Certainly there are in the connective tissue of the corium and in the subcutaneous tissue highly differentiated, complex, encapsulated nerve terminal which might well be excitable by the stronger external stimuli or perhaps equally well by stimuli within the tissues themselves from movement of the soft parts in conformity with postural changes in the body or extremities.

Without definite knowledge of the function of many of these borderland endings, it is possible to make only a presumptive classification and I have ventured to include among the proprioceptors all afferent nerve terminals, free and encapsulated, situated in mesoblastic tissue, which do not contribute any collateral branches to purely epithelial structures. In this classification one finds situated in the subcutaneous and deeper tissues the end-bulbs of Krause, the specialized endings of Ruffini and the Golgi-Mazzoni corpuscles, and in the proprioceptive field proper the neurotendinous end-organs of Golgi, the neuromuscular bundle, the specialized endings in the extraocular muscles, and on or among the skeletal muscle certain free terminals which have been described as interstitial sensory, pencil or brush-like, and basket-like endings.

Although an objection might be made to the inclusion of the Krause end-bulbs, the Ruffini end-organs, and the more superficial placid Pacinian bodies, all of which are no doubt subject to certain forms of external stimuli as well, there still remains a variety of terminals in the deeper tissue which might be more properly admitted in a study of the comparative morphology of the deep proprioceptors. These vary widely in form and structure and the individual variations might be comparatively studied in a given species of animal, or one or all of these endings might be studied phylogenetically throughout the animal series. Neither the time nor available material will permit an investigation so comprehensive as the strict comparative morphologist might demand, and I shall first describe very briefly the different forms of nerve terminals found in the deeper tissues without regard to

the animal species, and later review such knowledge as we possess concerning the more familiar nerve endings in muscle, tendon, and interstitial connective tissue with special reference to the comparative morphology of the muscle spindle or neuromuscular bundle in man and the lower animals.

The end-bulbs of Krause (fig. 81) are situated chiefly in the skin and conjunctiva and resemble very closely the well known Pacinian body which is found in the superficial and deeper tissues beneath the corium skin. The Krause endings are encapsulated terminals with a central non-medullated axis-cylinder terminating in a bulbous



FIG. 81. Krause end-bulbs (Barker)

enlargement without contributing any filaments to the epithelium. Although they generally are thought to receive tactile impressions and accordingly should be classed among the exteroceptive organs it is not unlikely that they might be stimulated by impulses originating in the subepithelial tissue from movement of the soft parts.

At the junction of the corium and subcutaneous tissue, often parallel to the surface and also situated more deeply in the areolar and fatty layers one finds the beautiful nerve terminals described by Ruffini (fig. 82). In these encapsulated organs the nerve fiber, as in the muscle spindle, enters the capsular sheath near the equator or from one of the poles and then divides into many complex terminals

arranged quite like those in some types of the Golgi neurotendinous end-organ. The Ruffini endings are found especially in the skin of the finger tips and although little is known of their function, their deposition in the deeper tissues as well and the strong connective tissue sheath which surrounds the nerve terminals suggest that they, like the neuro-muscular bundle, might be subject to mechanical stimulation, and thus serve a proprioceptive function.

Closely related to the Pacinian body, the end-bulbs of Krause, and the Golgi neurotendinous end-organ are the Golgi-Mazzoni corpuscles



FIG. 82. Ruffini end-organs (Barker)

(fig. 83) also described by Ruffini who found them in the subcutaneous tissue of the finger tip and on the sheaths of tendons. All of these terminals, the endings of Ruffini, Krause, Golgi-Mazzoni, Pacini and the Golgi end-organ (fig. 84) are closely allied in form and structure and it is assumed that they might subserve a similar function. For these reasons, I have ventured to refer to these more superficial endings together with those more deeply situated in tendon, muscle and joint, and generally regarded as proprioceptive organs.

Although many of these terminals have been found in man and in

the lower vertebrates I shall confine my study of their comparative morphology especially to the neuromuscular bundle or muscle spindle, and refer briefly to the epimysial and perimysial or interstitial sensory nerve endings in the lower animals in which the more highly specialized endings have not been discovered.

It will be helpful to describe first in a general way the normal muscle spindle as it occurs in the human being. Here it is usually found



FIG. 83. Golgi-Mazzoni corpuscles (Barker)

imbedded in the surrounding muscle tissue and parallel to the extra-fusal fibers. It contains two or more, sometimes as many as eleven, muscle cells enclosed in a lamellated connective tissue capsule of fusiform shape. In the equatorial region the muscle fibers often lose their striations and contain a deeply staining mass of nuclear material. The nerve and blood vessels ordinarily enter the capsule at the equator, whereupon the nerve soon loses its myelin sheath and ends in a



FIG. 84. Neuro-tendinous end-organ of Golgi from intercostal muscle of the cat. Gold chloride preparation (original).

complex network of terminals upon and about the muscle bundle. The variety of nerve-endings has been studied in detail by Ruffini who found them disposed in annular, spiral, or flower-like arrangements.

The neuromuscular bundle was first discovered in the frog and soon thereafter in the snake and the lizard since when it has been found in several species of birds and mammals; and its appearance in the adult human as well as in the fourth month of intrauterine life reveals little or no difference in form and structure from that observed in the lower species. I have found no record of the occur-



FIG. 85. The human muscle spindle from a case of paralysis agitans. Normal in all respects except for slight distension of the capsule in the equatorial region. Gold chloride preparation (after Byrnes, *Arch. Neurol. & Psych.*, 1926, xv).

rence of the spindle in animals lower than the vertebrates and in this division many classes have been studied. Thus among the amphibians a variety of teleosts, selacians, urodels, anoures, and cyclostomes have been examined, while in the class of reptiles the tortoise, snake, and lizard have furnished many beautiful specimens. Among the birds, the spindle has been demonstrated in the tom-tit, sparrow, magpie, heron, falcon, owl, stork, chicken, and pigeon, and

many specimens have been obtained in the mammalia from the rat, guinea-pig, pig, rabbit, cat, dog, ox, porcupine, fox, monkey, chimpanzee, and man. My own studies have been confined to an examination of the earthworm, goldfish, cat, guinea-pig, and man; and although nothing resembling a spindle was discovered in the earthworm, I found many of the well-known basket-like nerve terminals in the dorsal musculature of the goldfish, and it seems that these structures possess some of the features comparable to the more highly differentiated neuromuscular bundle.



FIG. 86. Muscle spindle of the cat (Renaut and Regaud)

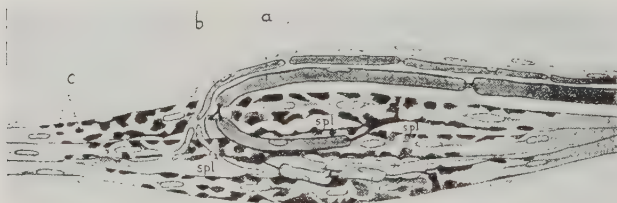


FIG. 87. Central portion muscle spindle of the pigeon (Renaut and Regaud)

It is remarkable that throughout the several classes of vertebrates the spindle varies only slightly in its morphology. It is always readily recognized by its fusiform shape; it is always encapsulated, and contains one or more differentiated intrafusal muscle fibers, upon which the specialized nerve endings terminate. These slight differences in structure are more readily portrayed in a series of illustrations than from a detailed description, and more easily understood if presented in the inverse zoölogical order.

When the mammalian spindle as it occurs in man (fig. 85) is compared with that found in the cat (fig. 86) there is a striking similarity in size, form, and structure. In the cat the capsule is not so

thick as that in man, but both spindles contain a number of intrafusal muscle fibers about which the nerve terminates in the anulo-spiral arrangement with secondary flower-like endings common to this class of mammals.

• In birds a specimen from the chicken or the pigeon might serve as standard for comparison; and here (fig. 87) the spindle is still pluri-

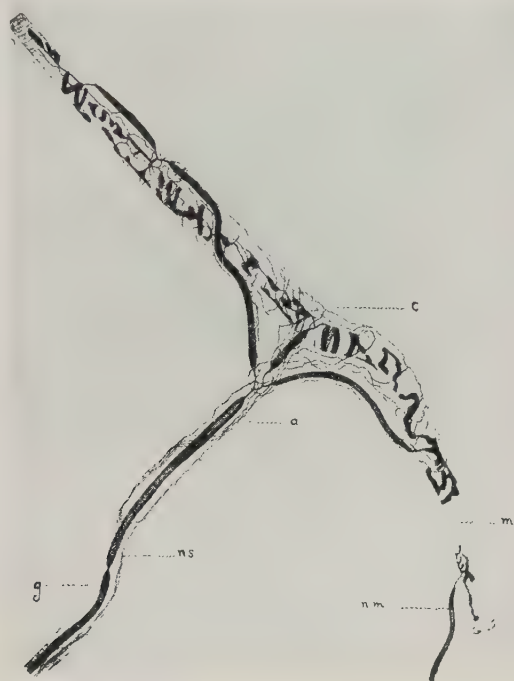


FIG. 88. Muscle spindle of a lizard (Renaut and Regaud)

fascicular, but the number of lamellae in the capsule is greatly reduced, and the large intrafusal nerve terminates more often in characteristic enlargements parallel to the muscle fiber rather than in the annular or flower-like arrangement common to the mammalia and the muscle fibers have, as usual, lost their equatorial striations.

The spindle in reptiles, represented by a specimen from the lizard (fig. 88), retains all of its essential components but these are evidently

arranged in a simpler fashion. The intrafusal muscle said to be always unifascicular preserves its equatorial striations and the nerve endings are usually simple but may be complex and abundant. As a rule, the nerve terminates in a polymorphous fashion in which there is preponderance of terminations *en fleurs*, regarded as distinctive of the reptilian ending although anular and spiral forms are sometimes observed. In the snake (fig. 89) a still simpler structure is found.

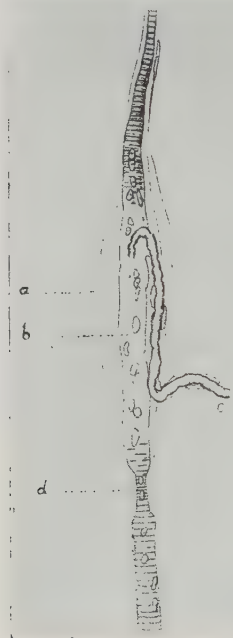


FIG. 89. Central portion muscle spindle of an adder (Renaut and Regaud)

The spindle is still unifascicular and often unipolar but the single muscle fiber has lost its equatorial striations and the capsule is thicker and more frequently laminated than in the lizard.

Of the amphibians, the frog occupies a unique position in the history of the muscle spindle. The neuromuscular bundle is said not to have been found in any of the tailed amphibians and of the tailless members of this class the frog is the only representative which has been studied. Here, the spindle, as in reptiles, is simpler in structure than in the

higher animals and although unifascicular specimens have been found there are, as a rule, two or more intrafusal muscle fibers which are devoid of striation in the equatorial region.

Although the neuromuscular bundle retains a fairly constant form and structure throughout the animal series from amphibia to mammalia there are, in the several species, slight variations which are thought to be distinctive. Thus, in the frog the spindle is usually plurifascicular, the striations are generally lost at the equator, and the central nuclei are arranged in both an axial and marginal fashion, but the anular and anulo-spiral endings are said not to occur. The neuromuscular bundles are distributed throughout most of the musculature and are especially abundant in the pectoral region, but they have not been found in the dorsal musculature where they appear to be replaced by the epimysial sensory ending quite analogous to those found in fish and other tailed amphibians; and, it is furthermore significant that the dorsal musculature in the frog has partly retained the metameric arrangement common to the urodelas and lower vertebrates.

It is surprising that the simplest form of the spindle is found in reptiles, where it is always unifascicular, frequently unipolar, and of uniform diameter throughout with consequent loss of its fusiform outline. This is especially true of the lizard, in which the spindle capsule consists of only one lamella without an equatorial dilatation although the intrafusal muscle retains, as a rule, its equatorial striations. In the snake, the capsule is slightly thicker and expanded at the equator; the single muscle fiber has lost its central striations and the intrafusal nerve terminates in short or long endings with terminations *en fleurs* predominating.

Both unifascicular and plurifascicular spindles are found in birds with the two types often occurring side by side. The intrafusal fibers retain their equatorial striations; they are very slender and much smaller than those in any of the vertebrates but of the same general character as in the tailed amphibia and reptiles. The capsule varies in thickness and is often pierced in definite zones by several nerve fibers which end in an abundant and complex group of terminals. Here, also, the spindle is widely distributed in the skeletal muscles but exhibits a tendency to occur in increasing number in the proximity of tendons and aponeuroses.

It is in mammalia and especially in the lower animals of this class

that the spindle has been most extensively studied. Here it is almost always bipolar, spindle-shaped, plurifascicular, and enclosed in a well defined capsule composed of several lamellae. Usually two nerves penetrate the capsule, one in the equatorial and the other at one of the polar extremities, and after encircling the muscle bundle in an annular or anulo-spiral fashion they terminate in occasional endings *en fleurs*.

Aside from these minor structural peculiarities in the different species, the spindle exhibits in the different zoological orders interesting variations in its distribution in the musculature and in its anatomical relations. Thus, in man it is said to occur in a ratio of about 1 to 100 extrafusal fibers and the total number has been estimated for several of the muscles. In the biceps brachii 69 have been counted but the omohyoid is said to contain as many as 30 or almost one-half the number in the entire biceps. Not more than 8 were found in the sartorius of the rat although they are abundant in the small muscles of the extremities. In the rabbit 18 have been found in the external pterygoid and 40 in the masseter. Huber counted from 60 to 100 in the upper intercostal muscles of the cat and observed that the spindles diminished in number in the caudal direction so that only 28 were discovered in the eleventh, and 18 in the twelfth interspaces respectively. The same relative ratio was found in the internal and external intercostals. It is thought that there might be slight variations in the total number of spindles in the different species of animals, and although studies of this character have not been extensive it is stated that the cat actually possesses a greater number of spindles in proportion to the extrafusal fibers than does the rabbit or guinea-pig. This observation has led to the opinion that the number of spindles is greater in the animal in which the muscle sense is more highly developed; and in this respect Regaud and Favre make the interesting statement that, "Il est très vraisemblable que le nombre des fuseaux est plus considérable chez les animaux dont le sens musculaire est très développé, comme le chat. Nous allons voir en effet que, pour une espèce donnée, les fuseaux prédominent dans les muscles affectés aux mouvements délicats qui exigent une coordination et une souplesse d'appropriation au but particulièrement précises." It seems that the spindles do not increase in number in proportion to the age of the animal. They are very numerous in the sixth month of foetal life and are said not to increase in numbers thereafter nor do

they increase in size consequent upon occupational exercise as do the extrafusul muscles. Although the spindles vary in number in different muscles in a given species or genus, they are uniformly more numerous in the muscles of the extremities than in those of the trunk, neck, or head, and also more abundant in the upper than in the lower extremities. Fraenkel found them in great numbers in the small muscles of the hand, in the flexors of the hand and fingers, and in the quadriceps femoris. Sherrington also found many beneath the aponeurosis covering the vastus internus, and in the small muscles of the feet.

Thus, while the spindle is widely distributed and particularly numerous in certain groups of muscles, there are several regions in which they are demonstrated with great difficulty or, indeed, said not to occur. It is asserted by some that they are not found in the extra-ocular muscles, but Sutton discovered them in these muscles of the embryo pig, and Crevatin demonstrated them in the eye muscle of the ox and later in other mammals. It is well known, however, that the end-organs of Golgi are abundant in the extra-ocular muscles, and it is suggested by those who deny the presence of the spindle in this region that function has been assumed by the Golgi terminations. There is likewise much dispute concerning the occurrence of spindles in the tongue musculature. Franque claims to have found them in the tongue of man, but does not state whether they were discovered in the extrinsic or the intrinsic muscles; and although Langworthy found them in the extrinsic tongue musculature he was unable to demonstrate them in the intrinsic group; and as many as thirteen spindles have been counted in a single cross section of the hyo-genio-glossus in man.

According to Sherrington, Cipallone, and Baum the muscles of the larynx contain no neuromuscular bundles, and the striated musculature of the oesophagus, although not under voluntary control, seems not to have been examined in this respect. The diaphragm is also said to be devoid of spindle, but Dogiel found them in this muscle in several species of animals. Baum failed to find them in the muscles of the pavilion of the ear, in the digastric, the stylo-hyoid, or the ischio-bulbocavernosus, and many unsuccessful efforts have been made to demonstrate them in the facial musculature.

In the course of its development the spindle exhibits interesting peculiarities. The intrafusul fibers have a more precocious development than in the surrounding muscle, so that the muscle bundle and

entire structure of the spindle are fully developed at the sixth month of foetal life. Weiss and Dutil found that in the embryo guinea-pig the sensory nerve to the spindle and to the end-organ of Golgi were fully developed when the motor terminals to the surrounding muscle were only incompletely formed, and Ruffini states that the nerve terminals in the spindle of a new-born child are already advanced to a degree equal to that observed in the spindle of an adult cat.

There are in the tailless amphibia and lower orders a variety of deep nerve terminals quite different from the motor endings. These are thought to convey afferent impulses of a proprioceptive nature and it has been suggested that these more primitive non-encapsulated terminals might be the analogues of the more highly differentiated neuromuscular bundle. Among these terminals one finds, according to Regaud and Favre, perimysial endings represented by the free non-myelinated terminals of Koelliker, and certain interstitial termi-



FIG. 90. Epimysial terminations en grappes; extraocular muscles of rabbit (Renaut and Regaud).

nals which resemble very closely the non-encapsulated end-organ of Golgi and the encapsulated Pacinian body. These interstitial terminals are also found in many mammals, and not only in the muscular tissue and their tendinous insertion, but also in the pleura, peritoneum and other tissues, so that, in all probability, they are not solely of proprioceptive function. The epimysial organs include the non-medullated nerve fibers ending directly upon or surrounding the muscle tissue, the terminations *en grappes* (fig. 90) with their ultimate endings surrounded by a nuclear mass of sarcolemma cells resembling the special type of endings in the ocular muscles (fig. 91), and the interstitial basket-like terminals (fig. 92) abundant in the tailed and tailless amphibia; and, finally, to this class also belongs the muscle spindle of the higher animals. Furthermore, certain pencil or brush-like (*en pinceau*) terminations are found in some of the selacians, in the shark and the ray fish; these have some resemblance to the muscle



FIG. 91. Special endings in extraocular muscles (Renaut and Regaud)



FIG. 92. Terminations en paniers (Renaut and Regaud)

spindle in that the endings are surrounded by an accumulation of nuclei and the muscle fiber exhibits in these areas slight structural changes.

The terminations *en paniers* are particularly common in fish, selacians, teleosts, and tailed amphibia, and I found many of them in the dorsal musculature of the ordinary goldfish. It is of special interest that while these endings are widely distributed in the musculature of the larvae of many of the anures, they are, in adult life confined to the dorsal musculature. Not infrequently these basket-terminals surround several muscle fibers and appear to enclose them in a fashion resembling the muscle bundle although there is no evidence of a true capsule.

Although form and function are closely related this does not, strictly speaking, warrant a digression into a consideration of the physiology of the muscle spindle. It is, nevertheless, of interest to recall that Cajal is of the opinion that the spindle might serve at a dynamometer or an automatic register of muscle contraction, and from my study of this organ in paralysis agitans, I suggested that it might possess an afferent inhibitory action upon muscle tone by integration of the innumerable sensory stimuli conveyed to the central nervous mechanism, and, furthermore, that there was no evidence to indicate that it has anything to do with the transmission of muscle sense.

Whatever the function of the spindle, it is evident from its absence in the tailed amphibia and lower orders that it is not essential to complete cerebellar activity in the lower animals and presumably that the impulse conveyed by this deep proprioceptor is designed for the more delicate and complex muscular activity of the higher orders. It seems, therefore, that the knowledge of the tonic state of the muscle below and including the anures might be conveyed by the simpler afferent nerve endings in the empimysial and perimysial tissues.

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CHAPTER VII

THE COMPARATIVE MORPHOLOGY OF THE MEMBRANOUS LABYRINTH AND THE LATERAL LINE ORGANS IN THEIR RELATION TO THE DEVELOPMENT OF THE CEREBELLUM¹

O. LARSELL, M.D.

THE cerebellum has its inception as a specialization of the cutaneous centers in the rostro-lateral region of the medulla oblongata. The studies of Johnston (1, 2) on *Acipenser* and *Petromyzon* have shown that the dorsal horns of the spinal cord, the acusticum of the medulla oblongata and the cerebellum, are continuous one with the other. In the cyclostomes, as represented by *Petromyzon*, the relations of these parts are very primitive. The tuberculum acusticum (area statica of Kappers, area octavo-lateralis of Herrick) which, as in selachians and ganoids, includes the lateral line lobe, merges caudally into the spinal V nucleus and the funicular nuclei in such a manner as to be indistinguishable from them caudally. With the entrance into the medulla oblongata of fibers from the specialized sense organs of the lateral line and vestibular systems, however, there occurs a modification in the structure of the oblongata. This modified region appears to correspond to the cerebellum bulbare of Tilney (3).

In *Petromyzon* the vestibular and lateral line organs are very simple, although representing a great advance over the general cutaneous sensory terminations. The organs of the lateral line system consist of simple pits or neuromasts or neuro-epithelium, which open onto the surface of the head and body regions. The pit organs of the head are innervated by the lateral line VII or lateralis anterior nerve. Those of the trunk receive their nerve fibers from the lateral line X or lateralis posterior nerve.

The vestibular organ (fig. 93) is more complex in its structure, although simple as compared with that of higher vertebrates. In

¹ From the Anatomical Laboratory of the University of Oregon Medical School, Portland, Oregon.

Petromyzon (4) it consists of a *saccus communis* which has two divisions, a vestibule and a sac-like appendage. There are but two semicircular canals, the anterior and the posterior which receive the ramus anterior and the ramus posterior of the VIII nerve respectively. Other fibers of this nerve pass to the *saccus communis*.

It is the fibers from these organs which enter the octavo-lateral area. Here they form centers of correlation and some pass rostrally to the region of the cerebellum. At the level of the VII and VIII root complex Johnston found a differentiation from the more generalized condition of the spinal V and funicular nuclei into three nuclei

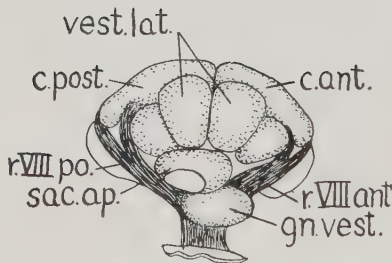


FIG. 93

FIG. 93. The labyrinth of *Petromyzon*. Modified from Retzius.

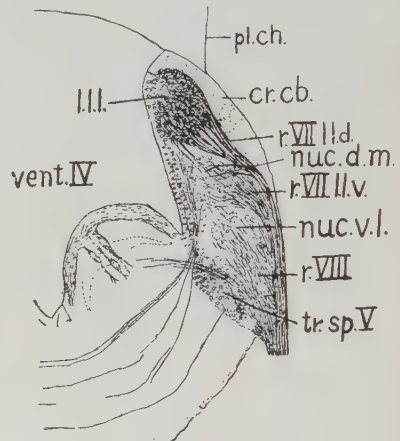


FIG. 94

FIG. 94. Transverse section at level of VII and VIII roots of medulla oblongata of *Petromyzon*. Modified from Johnston.

(fig. 94) which receive the lateralis and vestibular fibers. These he designates as lateral line lobe, dorso-median nucleus and ventro-median nucleus of the acusticum, respectively. Dorsolateral to the lateral line lobe and the dorsomedian nucleus, and partly extending between them, there is present a layer of fine fibers which Johnston considers homologous with the cerebellar crest of fishes. It is in these nuclei and the related layer of fine fibers that we may find the beginnings of the specialization which leads to the development rostrally of the cerebellum.

The lateral line lobe (nucleus dorsalis of Kappers) receive anterior

lateralis fibers, chiefly of the dorsal lateralis anterior root. The dorso-median nucleus (nucleus medialis of Kappers) receives both lateralis anterior and lateralis posterior fibers with the latter predominating. The ventro-lateral nucleus (nucleus ventralis of Kappers) while receiving some fibers of the lateralis anterior, is principally the nucleus of the vestibular division of the VIII nerve. The fibers which enter this nucleus end in part in connection with the spindle cells of the nucleus, with and without branching, and in part bifurcate into ascending and descending fibers. The descending fibers are considered homologous with the spinal VIII tract of higher vertebrates. The ascending fibers pass in large part to the cerebellum, where they end in the granular layer. This is the primitive direct vestibulo-cerebellar tract.

The dorsomedian nucleus, which is chiefly the nucleus of the posterior lateral nerve, and the ventrolateral nucleus, which is chiefly vestibular, enter into the formation of the granular layer of the cerebellum, while the layer of fine fibers, the crista cerebelli, continues rostrally as the molecular layer of the cerebellum. The acusticum is thus in direct continuity with the granular layer, while the molecular layer of the cerebellum extends caudally over the acusticum.

The cerebellum of *Petromyzon* has reached a stage of differentiation only very slightly above that of the octavolateral area. Johnston regarded it as only a dorsal fusion or bridge between the two acusticae (cerebellum jugale of Tilney), except that a small bundle of fibers enters it from the inferior lobes of the forebrain. This bundle marks the beginning of the cerebellum as a coördinating center, but no other tracts appear to enter it from in front.

The forerunners of the Purkinje cells in the cerebellum are almost identical with cells in the dorsomedian nucleus of the octavolateral area. Internal arcuate fibers of the cerebellum and of the octavolateral area have so gradual a transition that they cannot be distinguished unless traced to their cells of origin.

Summarizing we may conclude the account of the cerebellum of *Petromyzon* in the words of Kappers (5), that it "is clearly a continuation and further differentiation of the static area." As compared with some of the higher vertebrates, the static or octavolateral area is very simple, in keeping with the relatively small and little specialized sense organs the nerve fibers of which pass into this region of the oblongata.

AMPHIBIANS

The amphibians have the great advantage to the student of the cerebellum of presenting this organ in various stages of phylogenetic development in the adult forms of the various groups, and of recapitulating this development to a large extent in the larval stages of the higher urodeles and of Anura. At the same time it functions almost from its first appearance in these larvae. In some of the lower urodeles the presence of the cerebellum has been denied by some writers. It is present, however, although in more primitive condition even than in *Petromyzon*, in some respects, as Herrick (6) has pointed out. In the higher salamanders and in the anurans it is represented in simple form, but much beyond the cyclostomes in development.

In amphibians there is also present a lateral line system, which is retained throughout life in the urodeles but disappears at metamorphosis in the anurans. In the tadpole and adult stages of the frog (7, 8) we have an epitome of the changes which have occurred from the beginning of cerebellar formation in vertebrates to a simplified expression of the condition in the air-breathing vertebrates in which the lateralis system has been lost and only the vestibular system remains.

Herrick (6, 9) has described the process of formation of the definitive cerebellum in amphibians by fusion of the auricular lobe with the corpus cerebelli, and the writer has followed the stages of development in the tree frog, *Hyla regilla*. For the sake of clearness the principal steps of cerebellogenesis may be briefly reviewed as found in *Hyla* (8).

In the young larva the roof of the rhomboid fossa is entirely membranous. At stages of 16- to 18-mm. total length (fig. 95) there is present in the mid-region, which come later to be occupied by cerebellum, an oblique membranous plate. This is continuous caudally with the chorioid plexus of the IV ventricle, and laterally with the rhombic lip. Rostrally it continues in part with the anlage of the midbrain, which in the 16-mm. *Hyla* is also membranous near the mid-line. Rostrolaterally, however, the membranous covering is continuous with a swelling of massive tissue which rises up from the floor of the rhomboid fossa. This eminence is continuous with the tegmentum of the medulla oblongata. It represents the anlage of the corpus cerebelli. Medial and slightly caudal to the corpus cerebelli, and separated from it by a slight furrow at the 18-mm. stage, is

found a second slight swelling, the ventral cerebellar eminence, and caudal to both lies the eminentia trigemini. The rhomboid fossa extends laterally behind these swellings in its floor to form the recessus lateralis. Directly caudal to the cerebellar body, in the 18-mm. larva, and separated from it by the lateral recess, is found another swelling in the lateral region of the narrower portion of the fossa, namely the octavolateral area or area statica of Kappers. This is especially prominent at the level of the VII and VIII roots. The recessus

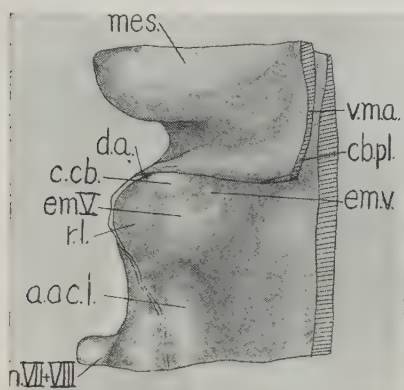


FIG. 95

FIG. 95. Dorsal view of model of cerebellar region of larval *Hyla* of 18 mm. The rhomboid fossa, anlage of the cerebellum and part of the mid-brain are shown.

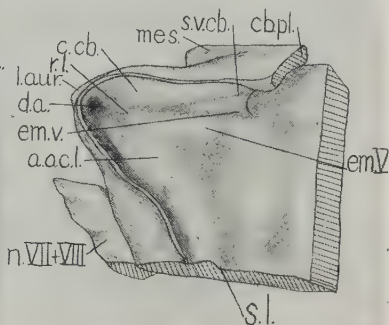


FIG. 96

FIG. 96. Dorsal view of model of cerebellar region of larval *Hyla* of 25 mm. The same structures as in figure 3, in more advanced development. (Both figures from Larsell, *Jour. Comp. Neurol.*, 1925, vol. 39, pp. 249-289.)

lateralis continues rostrally lateral to the corpus cerebelli, forming a pocket, the anterior diverticulum, which is covered with membrane.

In the 25-mm. larva (fig. 96) all the eminences named have increased considerably in size and extent. The ventral eminence is quite prominent and extends toward the midline. The corpus cerebelli has enlarged to such an extent as to form a definite rostral boundary for the rhomboid fossa, except medially, where the fossa continues into the aqueduct of Sylvius. By the 36-mm. stage the lateral portion of the body of the cerebellum over shadows the ventral eminence laterally, and a shallow depression, the floor of which constitutes a transition zone, separates the corpus cerebelli and the eminentia ventralis.

In the meantime the octavolateral area has also enlarged, chiefly by extending forward. The lateral recess has become relatively much

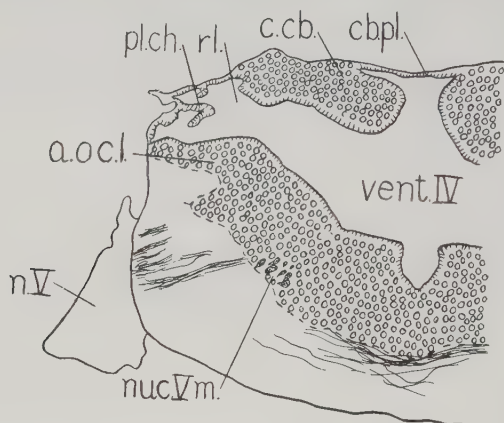


FIG. 97. Relation of auricular lobe, ventral cerebellar eminence, and the body of the cerebellum. Outline of section at caudal level of V root from larval *Hyla* of 36 mm.

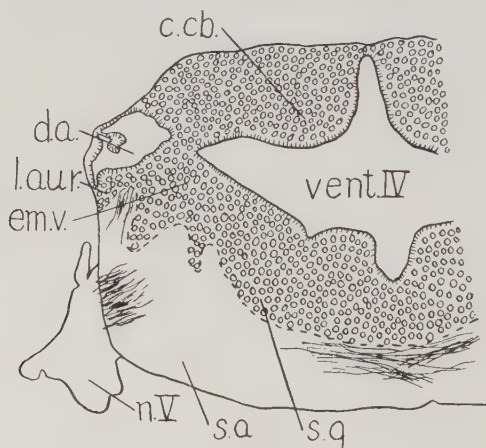


FIG. 98. Relation of auricular lobe, ventral cerebellar eminence, and the body of the cerebellum. Outline of section about midway between rostral and caudal levels of V roots in same larva.

narrower, due to the growth of the corpus cerebelli and the octavolateral area. Lateral to the anterior diverticulum a projection has

developed which is continuous with the lateral line lobe, and which constitutes the lobus auricularis. Between this and the corpus cerebelli there is a thin connection, made up however of nervous material. In the 36-mm. stage (figs. 97-99) this connection has become converted into a thick mass which is continuous ventrally with the tegmental gray. The lateral line lobe has also become prominent. The anterior diverticulum in this stage is reduced in relative size, due to the accretion of cells in its rostral wall.

A depression in the floor of the lateral recess still separates the octavolateral area from the corpus cerebelli and the eminentia ventralis, but this depression is narrower than in earlier stages. It is

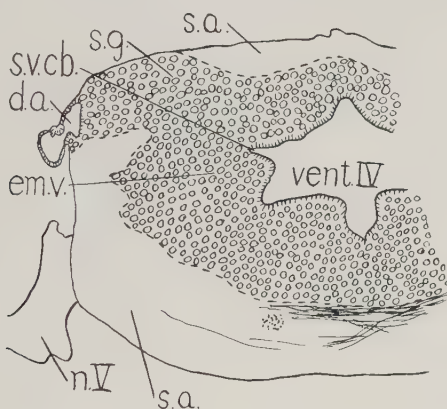


FIG. 99. Relation of auricular lobe, ventral cerebellar eminence and the body of the cerebellum. Outline of section at rostral level of V root in same larva. (From Larsell, *J. Comp. Neurol.*, 1925, xxxix, 249-289.)

the massive structures on either side of this furrow which represent the two anlagen of the definitive cerebellum, as Herrick has pointed out (6). The two stages of *Hyla* last described, namely, the 25- and 36-mm. total length larvae, represent an early and an advanced stage, respectively, in the process of fusion of the two component parts of the cerebellum. The cerebellum of *Necturus* (9) shows an external morphology somewhat more advanced than the 25-mm. *Hyla*, while the cerebellum of *Amblystoma* (10) is not so far developed as that of 36-mm. *Hyla*.

In the adult frog (*Rana*) the auricular lobe is greatly reduced in relative size, due to the dropping out of the lateral line system. The

corpus cerebelli has become so massive as to nearly obliterate the zone of fusion between it and the auricular lobe, but the relations of eminentia granularis, lobus auricularis and corpus cerebelli still remain and may be recognized from the internal structure.

The corpus cerebelli is formed on either side in early stages by a pushing upward of the rostral region of the tegmentum of the bulb, just caudal to the isthmus. This represents the region in which the spino-cerebellar fibers and the tracts from the midbrain meet, in later stages of development. The auricular lobes are formed by a forward continuation of the octavolateral areas and receive lateral line and vestibular fibers. In the further development of the tadpole, these two moieties fuse together across the floor of the lateral recess by increase of the ventral eminence in such a manner that a portion of the apparently external surface of the frog's cerebellum which formed the median wall and floor of the anterior diverticulum of the larva (figs. 98, 99), represents in reality a ventricular surface and is covered by a fold of the membranous chorioid plexus.

Rostrally the octavolateral area and the auricular lobe become in this manner continuous with the body of the cerebellum, and medially, under the floor of the lateral recess, they become continuous with the ventral eminence. The frog tadpole recapitulates so well the development of the cerebellum of urodeles that we may summarize the process of cerebellogenesis for the group as well as for the individual in the language of Herrick (6), namely, "the definitive amphibian cerebellum originates within the rhomboidal lip partly in front of and partly behind the lateral recess of the fourth ventricle; . . . these two regions come under the dominant influence of different functional connections (the first or body of the cerebellum by the spino-cerebellar system, the second or auricular lobe, by the vestibulo-lateral system); . . . in later development they fuse into a single massive organ. These two regions, moreover, in higher vertebrates retain something of their distinctive physiologic characters, becoming in one case the medial cerebellar mass and in the other case the lateral floccular part." With this description of the general relations between corpus cerebelli, ventral cerebellar eminence and auricular lobe in mind we may follow the changes which occur in the latter as they are related to the variations in the vestibular and lateral systems.

The lateral line organs of amphibians consist of simple neuromasts as in cyclostomes, arranged in well defined lines. In *Hyla* tadpoles

of 15 mm. greatest length, and probably earlier, the lateral line of the trunk and the head pits are already present. The latter however are poorly developed, as seen with the dissecting microscope. The supraorbital series of pit organs is usually visible in these small larvae, but the infraorbital organs are somewhat retarded in development, and appear only as traces at this stage. The pit organs of the trunk are well developed in the 15-mm. larva. By the 16- to 17-mm. stage all three lines are usually distinctly visible with low power magnification.

Sections of 16-mm. larvae and later stages, prepared by the Cajal method show the roots of the lateralis anterior and lateralis posterior

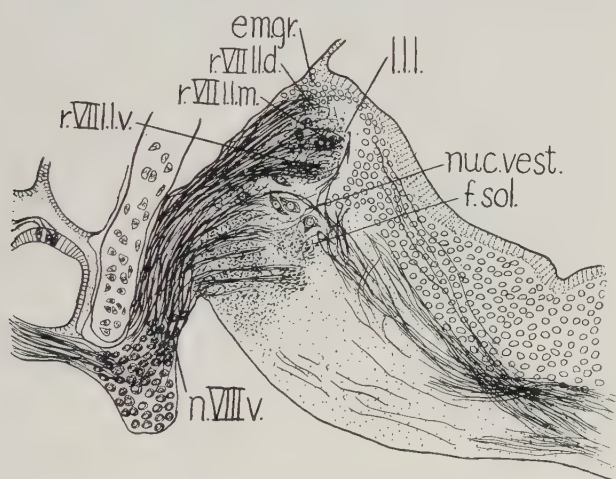


FIG. 100. Section of *Hyla* larva of 28 mm. total length, with no legs stained by method of Ramon y Cajal, cut at level of lateral line VII root, and showing lateral line lobe and related structures.

nerves (figs. 100, 101). The former are arranged in three bundles, a dorsal, a medial and a ventral. Only a single bundle of lateralis posterior root fibers is apparent at the 16-mm. stage, although in later stages a dorsal and a ventral bundle are found. These fibers represent the rostrally directed rami of the lateralis roots which enter the medulla oblongata. They form an area of neuropil which corresponds to Kingsbury's "dorsal island of alba," in *Necturus* (11), and which Norris (12) and Herrick (13) have shown to correspond with the lateral line lobe of fishes. In the floor of the rhomboid fossa this

lobe, together with vestibular fibers and nerve cells, produces a swelling, the octavolateral area (area statica of Kappers) which has already been described. This extends rostrally to form the auricular lobe, which by the 25-mm. stage is quite prominent.

The 36-mm. stage represents approximately the maximum development of the *Hyla* tadpole as a fish-like animal, for after attaining a length of 36 to 39 mm. it begins the process of metamorphosis. The

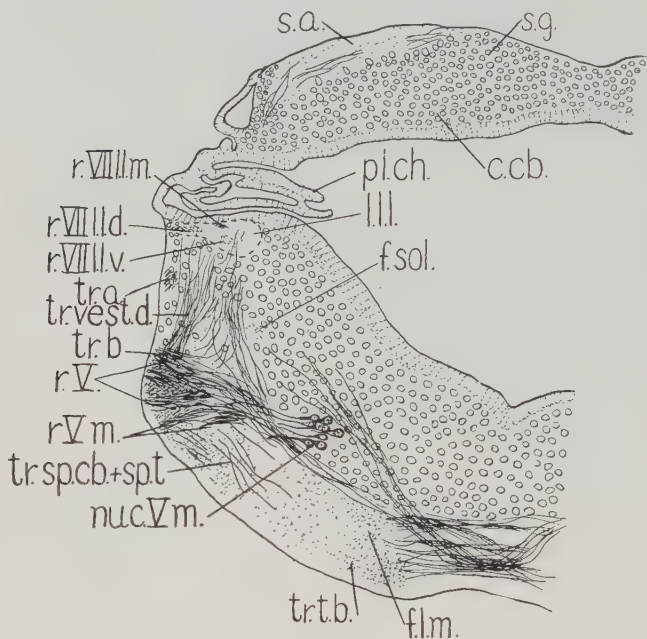


FIG. 101. Section at caudal level of V root in same larva, showing rostral region of lateral line lobe and the lateralis anterior and vestibular tracts in relation to it. (From Larsell, *J. Comp. Neurol.*, 1925, xxxix, 249-289.)

legs grow rapidly and the tail is resorbed. At the stage of 11-mm. tail length, at which the legs are well developed, the lateral line lobe begins to disappear in the acoustic area. Associated with this is the first sign, in tadpoles of 10- to 11-mm. tail length, of degeneration of the lateral line organs. These undergo regressive changes first in the head region. In nearly metamorphosed frogs of 3.5- to 1-mm. tail length the pit organs have all disappeared. Contemporaneous

with the regression of the pit organs there is a progressive degeneration of the lateralis anterior and posterior nerves. The lateral line lobe continues to decrease in size and eventually disappears just before metamorphosis is complete (figs (102, 103). This is accompanied by a relative reduction in the size of the auricular lobe, but the latter does not completely vanish because of the vestibular connections which will be considered below. These changes in the pit organs, the

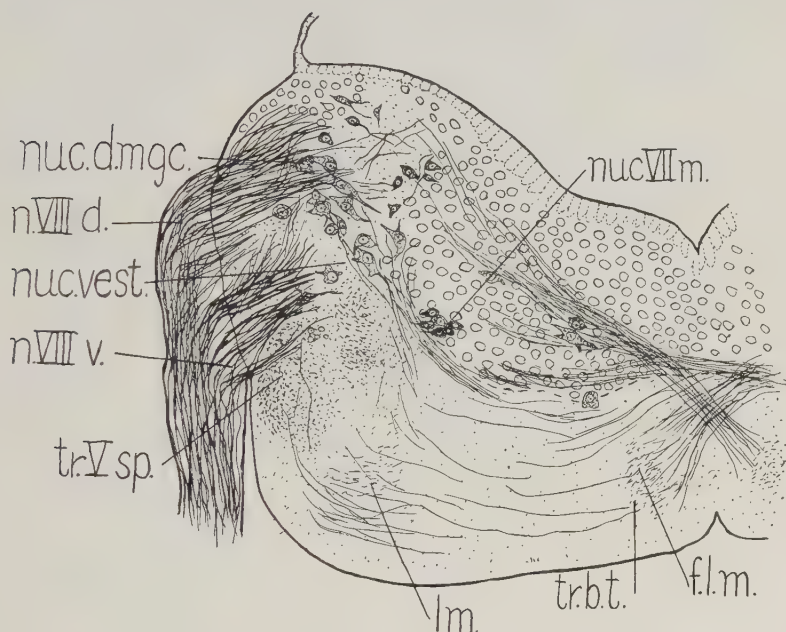


FIG. 102. Section at level of medulla oblongata of young *Hyla* with tail stump 1 mm. in length, taken at approximately the same level as shown in figure 103, but after disappearance of lateral line system.

lateralis nerve fibers and the central connections of the latter, are accompanied by chromatolysis of the ganglion cells of the lateral line VII (VIIb of Strong (14)) and lateral line portions of the IX and X ganglia. The first indication of chromatolytic change appears at about the 12-mm. tail stage, in which a few cells are affected, and is complete in young frogs of 3.5- to 1-mm. tail length, corresponding to the stages for complete disappearance of the pit organs and reduction of the lateral line lobe of the oblongata.

These observations are corroborated in a general way by Greene (15). This worker, using very young larvae of *Amblystoma*, extirpated the auditory placode unilaterally and bilaterally, and the head ectoderm of one side so as to include both auditory and lateral line

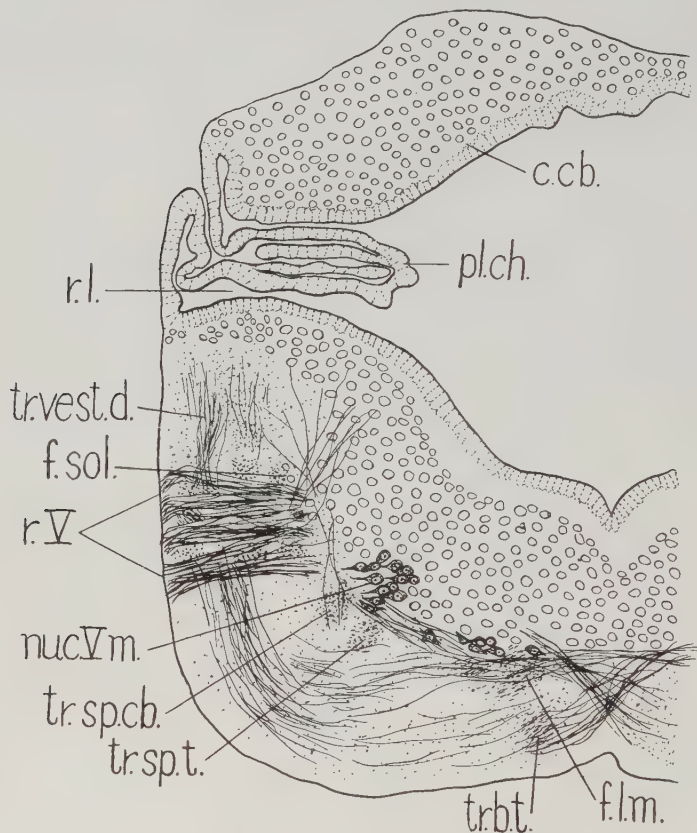


FIG. 103. Section at caudal level of V root in same larva as figure 102. Method of Ramon y Cajal. (From Larsell, *J. Comp. Neurol.*, 1925, xxxix, 249-289.)

placodes, in three series of larvae. He found that after raising these larvae to feeding stages that "the sensory nuclei and tracts of the medulla wall (area acustica lateralis) show progressive phases of a developmental loss in accord with the extent of extirpations in each series."

The vestibular labyrinth in Amphibia (fig. 104) shows definite advances in morphology above that of Petromyzon. Both urodeles and anurans have an ampulla anterior, ampulla posterior and ampulla externa, with corresponding semi-circular canals. In addition they all have an utriculus, a crista neglecta and a papilla lagena, all of which appear to serve the vestibular function. Of the fifteen representatives of as many genera of amphibians whose labyrinth is described by Retzius, all have in addition a papilla basilaris cochleae except *Proteus*, *Menobranchus* (*Necturus*) and *Amphiuma*. This is supplied by fibers from the dorsal ramus of the VIII nerve, as are the crista neglecta, the papilla lagena and the ampulla posterior.

The labyrinth of most amphibians is flattened and rather primitive in appearance, as compared with that of most fishes and reptiles. In the anurans, however, especially among the more active forms such as *Hyla* and *Rana*, the organ approaches more nearly the structural characteristic of fishes and reptiles.

To what extent the morphology of the amphibian labyrinth can be considered related to the degree of development of the cerebellum in these forms is not altogether clear. At least it can be said that both organs are larger and better developed in the more active representatives of the group. In this way they are undoubtedly related in differentiation. The relative importance of the vestibular system as a cerebellogenetic factor in urodeles and larval anurans, as compared with adult frogs, is hidden by the much greater size and importance of the lateralis connections in the first named forms.

In the adult frog (*Rana*) the auricular lobe, as already indicated, is much reduced, and only the vestibular connections remain. In addition to the vestibular fibers to the auricular lobe, *Rana* shows clearly that collaterals from such fibers pass to the transition zone of the ventral eminence. Some fibers of this tract also pass medially to end in the granular layer of the body of the cerebellum, and others appear to continue into the molecular layer, both of the same and the opposite side, decussating through the lateral commissure.

Herrick (6) has called attention to the presence of the anterior diverticulum in the adult frog. It is found in the same relation as in *Amblystoma* and larval *Hyla*, with plexiform lateral wall, rather than being bounded on all sides by nervous material. This is very obvious in my sections of newly metamorphosed specimens of *Hyla*, and a re-examination of series of adult *Rana* has convinced me of the

correctness of Herrick's statement here also, although the diverticulum is much more obscure in this material. The apparently lateral surface of the cerebellum in the adult frog is therefore a portion of the ventricular floor, as the cellular structure (*eminentia granularis*) substantiates. It is covered by membranous chorioid plexus. The frog's cerebellum accordingly shows the same general features as that of urodeles, but the region which receives spinocerebellar and cerebral connections is greatly increased, while the auricular lobe is reduced. The reduction of the latter very clearly accompanies the disappearance of the lateral line system.

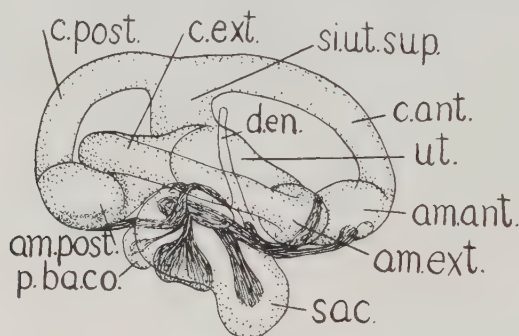


FIG. 104. Labyrinth of *Hyla pelobates*. Modified from Retzius

The cerebellar nuclei

The development of the nucleus cerebelli, which is the forerunner of the deep cerebellar nuclei, shows in the tadpole a very intimate connection with the anlage of the vestibular nucleus. The common origin of the vestibular and cerebellar nuclei has been suggested by van Hoever (16), Kappers (5) and others. In larval *Hyla* the continuity between the two is well shown (fig. 105). In Golgi sections of various stages the vestibular nucleus may be distinguished from the nucleus cerebelli only by its more caudal position. There is no line of demarcation between them, even in late stages, although in the latter the cells in the rostral part of the nucleus cerebelli are larger than elsewhere in the combined nuclear mass. Furthermore, the axones of these rostral cells pass forward to form the brachium conjunctivum. The axones from the caudal cells of the cerebellar part of the combined mass pass to the tegmentum of the oblongata as internal arcuate fibers.

Some of these are collected together as a cerebello-tegmental tract in older stages.

The cells of the caudal portion of the combined nucleus are of smaller size. It is this region which becomes the vestibular nucleus. The dendritic processes of these cells pass in large part lateralward and are distributed among the entering fibers of the vestibular nerve. Some dendrites of these cells comes into relation with various fiber

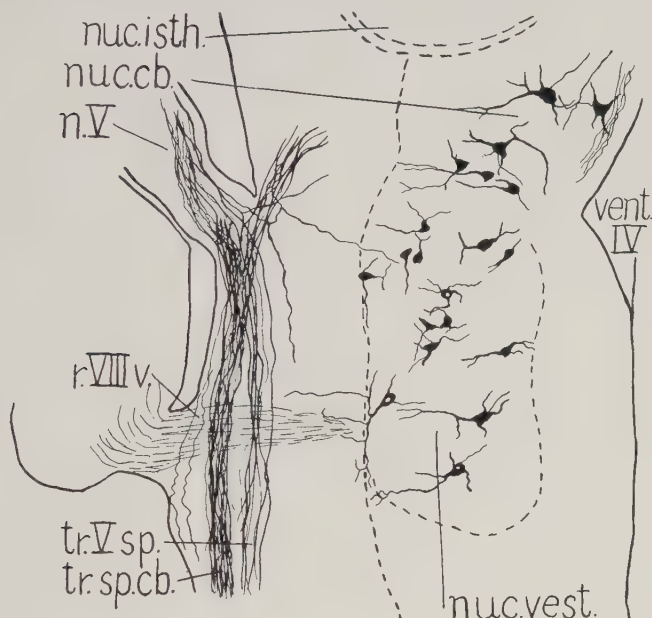


FIG. 105. Horizontal section of rostral region of medulla oblongata, showing nucleus cerebelli and nucleus vestibularis in *Hyla regilla* of 1 mm. tail length. Golgi method. (From Larsell, *J. Comp. Neurol.*, 1925, xxxix, 249-289.)

tracts of this region of the bulb, so that there is repeated in the frog larva the condition described by Herrick in *Amblystoma* (13). This holds true in more limited degree in older stages of *Hyla*, and was also found by the writer in the adult frog (*Rana*) in the transition zone from the bulb to the ventral cerebellar eminence. In this transition zone in *Hyla* are found various gradations, from cells whose dendrites do not appear to reach beyond the limits of the nucleus cerebelli to others whose widespread dendritic processes extend into the stratus alba of the oblongata.

The relation between nucleus cerebelli and nucleus vestibularis is further shown by the fibers which enter them respectively. The caudal portion of the vestibulo-cerebellar nuclear mass receives not only direct vestibular fibers, but also collaterals from the direct vestibulo-cerebellar tract. Furthermore the dendritic processes of many of the cells of the vestibular portion of the nucleus come into synaptic relation not only with the fibers of the vestibular nerve, but also with the spino-cerebellar tract. In the transition zone many of the cells send their larger dendrites into the spino-cerebellar tract, but some pass to the vestibular roots from this region also. The rostral region of the common nucleus receives collaterals from the spinocerebellar tract in the same manner as does the caudal region from the vestibular root. It received direct vestibular fibers as well.

It is this rostral region which receives the major share of spino-cerebellar impulses through the dendritic processes mentioned, in addition to the vestibular impulses, which differentiates into the nucleus cerebelli. It remains in the frog its continuity with the tegmentum ventrally, but in its growth extends upward more and more toward the body of the cerebellum and brings about the fusion of the ventral eminence with the corpus cerebelli.

It thus appears evident that from a common vestibulo-cerebellar nuclear mass in the region of the entering roots of the vestibular nerve there is differentiated the nucleus cerebelli and the nucleus vestibularis of amphibians. The nucleus cerebelli appears from its connections to be primarily a correlation center for vestibular and spinal stimuli. Both of these nuclei undergo further elaboration in the higher vertebrates and each becomes subdivided into several masses.

The vestibular nucleus may be omitted from further consideration, and attention focussed on the nucleus cerebelli. Van Hoesell (16) pointed out in some of the reptiles that there are two nuclear masses in the cerebellum, which he called the medial and the lateral cerebellar nuclei. This division I have been able to confirm in lizards and the garter snake (17), but in these reptiles it is not so marked as in the larger forms studied by van Hoesell. Direct fibers from the vestibular nerve appear to pass to the medial of these nuclei in the lizards and snake, as do also fibers from the vestibular nuclei. Many fibers from the latter terminate in the granular layer also. According to Kappers (5), direct vestibular fibers pass principally to the medial nucleus in the crocodile, and Allen (18) has clear evidence from his

degeneration experiments in the guinea-pig that the connections of this nucleus are chiefly vestibular, although in this mammal it may also receive spinocerebellar fibers and cortical fibers from the vermis.

Allen found that all the brachium conjunctivum fibers take their origin from the lateral cerebellar nuclei, while the fastigial nucleus takes no part in the formation of this bundle. The nucleus cerebelli of amphibians, the rostral most cells of which give rise to brachium conjunctivum fibers, must therefore be regarded as more than the primitive fastigial nucleus. It is rather the primitive nuclear mass from which both medial and lateral groups of cerebellar nuclei are derived. The medial or fastigial nucleus of higher forms retains the vestibular function which appears to be predominant for the entire nucleus cerebelli of amphibians. It should be regarded therefore as the most primitive of the cerebellar nuclei, and is the most closely related to the vestibular apparatus in the mammals. Stated differently, it is the medial cerebellar nucleus which is derived primarily from the vestibulo-cerebellar mass in the lower forms.

FISHES

Before passing on to a consideration of the vestibular apparatus and its cerebellar connections in the air-breathing forms above the frog, it will be instructive first to review briefly the lateralis and vestibular connections in selachians, ganoids and teleosts. In these groups although they are lower in the vertebrate scale than the amphibians already considered, the lateral line organs are greatly developed by comparison, and in some species this apparatus is greatly exaggerated.

The labyrinth (4), while more primitive than that of most amphibians in the absence of the pars basilaris cochleae, and in other features, nevertheless is well developed in all the fishes. It seems to be somewhat larger, relatively, than in amphibians, but has the same number of vestibular nerve terminals, if the pars basilaris cochleae of higher amphibians be considered acoustic. There is a difference in size of the nerve fibers from certain parts of the labyrinth in teleosts, which gives this group added interest, since because of this fact the central connections can more readily be followed. These two sensory systems and their connections will serve admirably in the fishes to check the interpretations based on Cyclostome and amphibian material.

Selachians

In the elasmobranchs, as compared with *Petromyzon*, the labyrinth is very large. It is also much farther differentiated, as shown by the presence of the third semicircular canal, the *canalis externa*, and by the subdivision of the *saccus communis* into *sacculus* and *utricleus* (4). The beginning of the *lagena* is also to be noted, and a *crista neglecta* is present. The VIII nerve in selachians accordingly has a much wider distribution than in *Petromyzon*. It passes into the oblongata in two bundles, the *ramus anterior* and the *ramus posterior*. Without entering into the details of the distribution of the fibers from these two bundles, since these have been well summarized by Kappers (5), it is sufficient to state that the *radix posterior* corresponds to the cochlear nerve of higher vertebrates and the *radix anterior* to the vestibular nerve.

The lateral line organs of elasmobranchs are well developed. Instead of the simple pit organs of cyclostomes and amphibians, the nerve endings of this system in selachians are enclosed in canals which open to the surface by pores at intervals. The fundamental similarity of the *lateralis* organs to the vestibular sensory apparatus has been shown by Johnson (19). In addition to the true *lateralis* system the sharks have related sensory organs in the head region, namely the ampullae of Lorenzini and the corpuscles of Savi. Altogether these three systems of related organs, together with the more highly developed vestibular apparatus, as compared with cyclostomes, give to the lateral line and vestibular systems and their central connections a much greater importance than in the cyclostomes and Amphibia. This is reflected in the greatly developed octavolateral area and the related auricular lobe in elasmobranchs in general, as compared with the two groups already considered. It is also shown by the fact that among the selachians the auricles are more developed in species with extensive and large lateral line organs than in others of equal body size but with smaller *lateralis* system.

The labyrinth of teleosts (4) differs from that of elasmobranchs in the closure of the endolymphatic duct and in the further development of the *lagena*. The number of vestibular nerve terminations remains the same as in the previous group. The large ampulla fibers and those of the *crista neglecta* pass directly to the tangential nucleus, in which also end the large fibered elements of the *lateralis anterior*

nerve. The large fibers from the utricle and saccule end in Deiter's nucleus and among the reticular cells, and are chiefly descending homolateral fibers. The remaining fibers, *i.e.*, part of the ampulla and saccule fibers and all the lagena fibers form ascending and descending tracts in the dorsal part of the octavolateral area, in which they terminate.

Direct vestibular fibers reach the crista cerebelli and the eminentia granularis in teleosts. Some of the saccule fibers, together with the fine fibered components from the ampullae and the lagena form an ascending (and descending) tract which in part reaches the cerebellum. In *Gadus*, *Arius* and *Pleuronectes*, Addison (20) was unable to find direct vestibular connections with the corpus cerebelli.

Among many of the teleosts the lateral line organs are unusually large and extensive. This is especially true in *Mormyrus* and some of the deep sea fishes. In many of the latter the head organs especially have an extraordinary development. With this hypertrophy of the peripheral organs is correlated very large nerve trunks and central connections.

The lateralis anterior fibers pass in large part into a dorsal nucleus of the octavolateral area, corresponding to Johnston's lateral line lobe in *Petromyzon*, but some reach the medial nucleus (dorsomedial nucleus of Johnston). Below this lies the ventral nucleus, which receives vestibular fibers. The same general relations hold therefore as in cyclostomes. A new feature, the valvula, appears in the teleost cerebellum, and in *Mormyrus* it is enormously exaggerated. In some fishes (21) the granular layer of the valvula is continuous with the eminentia granularis. Van der Sprenkel (22) concluded that this hypertrophy in *Mormyrus* is tied up with the extraordinary size and extent of the lateral line nerves and their connections in this form. It spreads out the ventricle of the midbrain and grows out in such a manner as to cover nearly all the remainder of the brain. In *Megalops*, in which the valvula is also greatly hypertrophied, it is continuous with the confluence of the lateral line lobes which occurs in this fish (fig. 106). Tello (23) found in the larval carp that ascending lateralis fibers of the lateral line VII nerve enter the pars postrema cerebelli. In *Gadus* however, according to Addison (20), these fibers terminate in the valvula and "thus establish a direct relation between the development of the valvula and the lateral nerve system." The valvula is to be considered as a forward continuation of cerebellar tissue related

physiologically to the paired cerebellar crests which extend caudally. We have herein the explanation of the unusual hypertrophy of the valvula in *Mormyrus* and other fishes in which the lateral line system is greatly hypertrophied. The eminentia granularis, which are already noted, is present in a reduced condition in amphibians, where it has a membranous roof, is prominent in Teleosts and corresponds to the auricles of elasmobranchs (6). It continues forward with the valvula.

It seems clear therefore that even the relatively complex cerebellum of fishes may be reduced to a median corpus cerebelli and a laterally placed vestibulolateral portion, corresponding to the auricular lobe. The latter varies in size and elaboration with the degree of development of the vestibulolateral sensory organs. The fishes therefore show clearly, some of them in an exaggerated manner, the intimate relationship between these systems of organs and the degree of development of those regions of the cerebellum with which they are connected. This is especially true of the lateralis system which shows the greater variation.

REPTILES

Among the reptiles the vestibular system alone remains, the lateral line organs and nerves having completely disappeared with the assumption of the land habitat. The VIII nerve is made up of a ramus posterior, which innervates sacculus, ampulla posterior, macula, lagena and papilla basilaris cochleae, and a ramus anterior, which innervates the ampullae anterior and externa and the utriculus. The forward vestibular bundle and the vestibular portion of the posterior bundle send their large fibers into a specialized portion of the vestibular nucleus, known as the tangential nucleus. Finer fibers arise from the sacculus and the utriculus and also as part of the ampulla bundles (5). These enter the oblongata and divide into ascending and descending rami. The ascending branches reach the lower cerebellar region, as in teleosts.

In the garter snake the auricular lobe is present as a very small lateral appendage (fig. 107), recognizable because of its vestibular (fig. 108) connections (17). In most lizards it is overshadowed by the development of the pars lateralis cerebelli, although in *Anniella* it is degenerated relatively even more than the remainder of the cerebellum. DeLange (24), Ingvar (25) and Kappers (5) recognize an auricular

lobe in the crocodilians, where it attains considerable size, but in none of the reptiles except the garter snake have vestibular fiber connections to the auriculus been described.

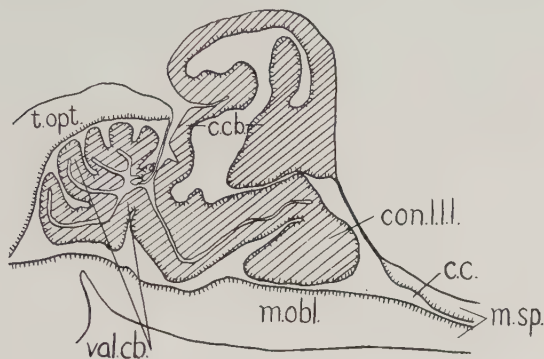


FIG. 106. Diagrammatic sagittal section of *Megalops cyprinoides*, showing relation of valvula and the concrescence of the lateral line lobes to other cerebellar structures. Modified from van der Horst.

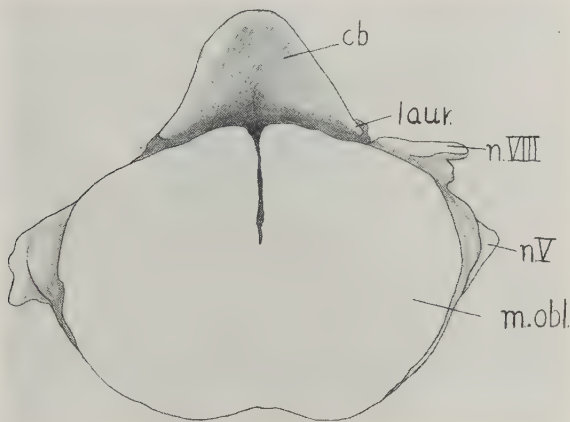


FIG. 107. Model of cerebellar region in garter snake (*Thamnophis sp.*). (From Lårsell, *J. Comp. Neurol.*, 1926, xli, 59-94.)

Ingvar observed in the crocodile and other reptiles that the vestibulo-cerebellar fibers, including direct and secondary tracts, end chiefly in the caudal two-thirds of the cerebellum, in both cortex and deep

nuclei. This I can confirm in general in lizards and garter snake. Ingvar found, moreover that the lobus posterior in the crocodiles is directly continuous with the auricles, so that while the auricles themselves have but little in the way of vestibular connections, the closely related posterior lobe is very important in this respect. It is evident that the auricular lobe itself plays a very minor rôle in the reptiles. This seems to be closely related with the complete absence

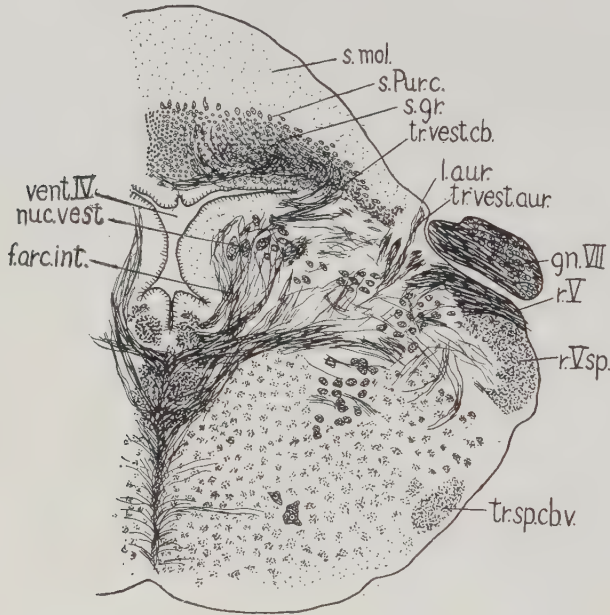


FIG. 108. Transverse section through cerebellar region of garter snake (*Thamnophis* sp.). Pal-Weigert stain.

of the lateral line system and the failure as yet of the vestibular apparatus and its connections to reach the importance in these forms which it has in birds and mammals.

The relation of the vestibular nerve to the nucleus cerebelli, so evident in amphibians, is again shown in the reptiles. We here find a differentiation of the nuclear mass into a nucleus cerebelli mediale and a nucleus cerebelli lateralis, and these are more completely separated from the tegmentum than in amphibians.

BIRDS

The cerebellum in birds is of the same pattern as in reptiles. Ingvar's analysis (25) shows the three primary lobes as in *Gerrhonotus* and the crocodilians, and in addition a well marked auricle (flocculus and paraflocculus). The cerebellum of the chick of five days incubation and later, described and figured (figs. 109, 110) by Ingvar, resembles closely the relations between cerebellum and auricular lobe in urodeles. The increase in size of the auricle in birds as compared

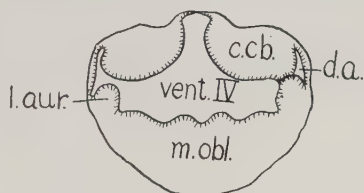


FIG. 109. Transverse section of the cerebellar anlage of chick embryo of five days' incubation. Modified from Ingvar.

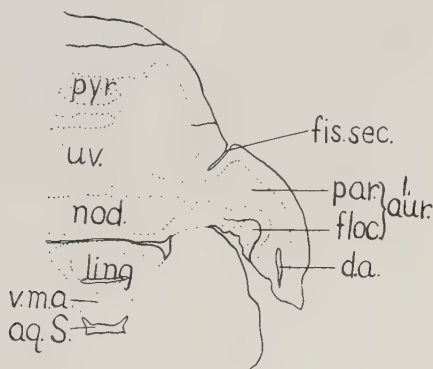


FIG. 110. Section through posterior lobe and auricle of chick. Modified from Ingvar.

with reptiles cannot be attributed to any marked modification, except in size, of the vestibular sensory apparatus. As in mammals, in addition to the flocculus, a paraflocculus was established by Ingvar. Both flocculus and paraflocculus are continuous with the posterior lobe, which consists of pyramis, nodulus and uvula.

The labyrinth of birds (4) is well developed and relatively is larger than in reptiles. In general it shows the same plan of arrangement

of fibers as in amphibians and reptiles. The lagena is well developed, but the cochlea, although larger than in reptiles, is not spiral as in most mammals. The vestibular nerve has various central connections, but a part of the vestibular fibers end in the cortex of the lower cerebellar region, thus forming direct vestibular connections and the cerebellum. The vestibular nucleus also sends axones to the caudal part of the corpus cerebelli and apparently to the flocculus.

The intimate relation of these connections to the development of the cerebellum is shown by an experimental observation of Greggio, cited by Ingvar (26). Greggio removed the vestibular apparatus in newly hatched pigeons and found as a consequence defective development of the cerebellum, particularly in the basal lamellae of the posterior parts. This observation is of great interest in connection with the experiments of Greene, already cited, on *Amblystoma* larvae.

The paraflocculus is first found in birds and is joined to the uvula. Whether or not the appearance of this division of the cerebellum is in anyway connected with the large labyrinth of birds is problematical. The possibility must be recognized in view of the relatively smaller size of both labyrinth and paraflocculus in most mammals.

MAMMALS

The labyrinth of mammals differs from that of birds chiefly in its somewhat smaller relative size, as just stated, and in the greater development of the cochlea. As the latter is concerned with the auditory sense rather than the vestibular, it may be dismissed from further consideration in the present connection.

In the light of the central vestibular connections in lower vertebrates, as indicated in the preceding pages, those of mammals are of great interest. Ingvar (25) has shown in the cat that direct vestibular fibers pass to the cortex of the flocculus, the uvula, and the nodulus of the posterior lobe and to the lingula of the anterior lobe. The direct ascending fibers give off collaterals to Deiter's and to Bechterew's nucleus. Such fibers also reach the fastigial nucleus, both homolateral and contralateral, and possibly, according to Ingvar (25, 26), the nucleus dentatus, although Allen (18) was unable to corroborate this connection. These fibers, of vestibular origin, may be regarded as the oldest phylogenetically, in the mammalian cerebellum, for they are present in the entire vertebrate series. Their connections must therefore be considered as the most ancient parts

of the cerebellum. The mammalian cerebellum accordingly has the same general pattern, so far as these vestibular connections are concerned, as that of birds. All of the above named parts are closely connected by position at the base of the cerebellum and all also lie close to the vestibular nuclei. Ingvar concludes that the basal portion of the cerebellum is predominantly vestibular, and forms a "calyx from which the remainder of the organ in higher forms has developed (26)." This interpretation agrees with the findings of comparative anatomy in lower forms of vertebrates, if it be kept in mind that in fishes and water living amphibians the lateral line organs in large part overshadow the vestibular connections in their effect on the morphogenesis of the cerebellum. In the mammals it is in close

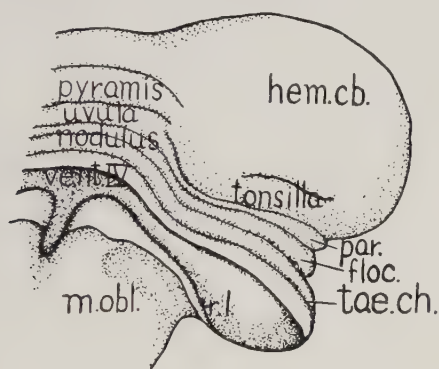


FIG. 111. Part of the cerebellum of human foetus of 12 cm., showing relations of flocculus and paraflocculus to nodulus and uvula. Modified from Ingvar.

agreement with the experimental results of Allen (18), who found in the guinea-pig that there are apparently two distinct functional groups of cerebellar nuclei. One group, the lateral, includes the nucleus dentatus and nucleus interpositus (nucleus emboliformis plus nucleus globosus); the second or medial group is made up of the fastigial nucleus. The lateral group receives no direct spinal or cranial nerve roots and no fibers from the spinal cord or the bulb, but apparently only fibers from the cerebellar cortex, especially of the hemispheres. The fastigial nucleus, on the other hand, receives chiefly vestibular fibers, as in lower vertebrates, both direct and from the vestibular nuclei. In addition it receives fibers from the cortex of the vermis probably from the basal vestibular cortex, and from

the cord. Its connections are thus predominantly vestibular and it apparently corresponds to the major portion of the primitive nucleus cerebelli of amphibians, whose relations to the vestibular nucleus have already been described.

The relation of the auricle (flocculus and paraflocculus) of mammals (fig. 111) to the uvula and nodulus, Ingvar describes as being essentially the same as in birds. The flocculus and paraflocculus are forced laterally, evidently by the development of the lobus ansoparamedianus, which Ingvar considers the specific mammalian part of the cerebellum. This lateral displacement, he states, reduces the connections of the paraflocculus with the frontal lamellae of the uvula, on the one hand, and of the flocculus with the lamellae of the nodulus on the other hand, to slender bands of myelinated fibers.

Bolk (27) found the flocculus and paraflocculus (termed by him together the *formatio vermicularis*) greatly enlarged in the whale. This fact, together with their intimate vestibular connections, already shown, would suggest a vestibular function, but extirpation of the large paraflocculus of the rabbit by Bárány (28), failed to produce disturbance of equilibrium. Whatever their functional significance may prove to be in mammals, their morphological derivation and relationship appears firmly established, and their relation to the auricle of lower vertebrates seems clear.

CONCLUSIONS

It is evident from the foregoing account that the cerebellum is the result of a gradual process of specialization from the more generalized nervous centers of the medulla oblongata. This process had its inception in the cyclostomes or their allies, by the differentiation of special nuclei for the lateral line and vestibular systems. In *Amphioxus*, which lacks these systems, no cerebellum is to be found. The lateral line and vestibular nuclei themselves, however, do not constitute the cerebellum or any part of it, although the line of demarcation is not easy to draw. It is only at the rostral end of these nuclear masses, where other stimuli, from the cerebral region and especially from the tectum, come into relation with the specialized stimuli from the bulbar region, that a correlation center is established.

The lateralis and vestibularis fibers end primarily in the auricle, in fishes and amphibians, and only to a lesser degree in the corpus cerebelli. With the increase in importance of the corpus cerebelli,

due to greater development of the spino-cerebellar and other cerebellopetal tracts, it spreads laterally and fuses with the auricles.

The importance of the lateral line and vestibular end organs, together and separately, and of their central connections in cerebellogenesis, is shown by the changes which take place in cerebellar structure with the loss of these organs during development, either by experimental procedure, as in *Amblystoma* and the pigeon, or naturally during metamorphosis of the frog. These changes are in complete accord with the phylogenetic and ontogenetic facts, and corroborate the latter in a striking manner.

The intimate genetic relationship of the primitive nucleus cerebelli to the vestibular nucleus points also to the importance in cerebellogenesis of the vestibular system.

With the loss of the lateralis organs in the land living forms and the assumption of relatively much greater importance by the spino-cerebellar connections, the auricular lobe is reduced in size in the reptiles. It reappears in larger size, however, in birds and mammals, and as the flocculus and paraflocculus is a well defined element of the avian and mammalian cerebellum.

The lateral line and vestibular connections may therefore be regarded as laying the foundations for cerebellar development. The vestibular cerebellum becomes more and more overshadowed in the higher members of the vertebrate series by the growing importance of other connections, particularly the spino-cerebellar, as already indicated, but it retains its basal position and primitive relations. In the mammalian and human cerebellum the vestibular portion includes part of the vermis, namely, the uvula and nodulus of the posterior lobe and the lingula of the anterior lobe. The flocculus and para-flocculus, which also belong to the posterior lobe of Ingvar, are connected with the uvula and nodulus, and are also to be considered as part of the vestibular cerebellum.

Bremer's definition of the paleocerebellum and neocerebellum, namely that the former is made up of the anterior and posterior lobes of Ingvar, while the latter corresponds to the medial lobe, is quoted with approval by Ingvar (26). In view of the close relationship of the medial nucleus to the vestibular cerebellum and in the light of its developmental history, it appears to the writer that this nucleus should be included in the paleocerebellum. This should then be defined as made up of the anterior and posterior lobes and the fastigial

nucleus. The neocerebellum should similarly, perhaps, include Ingvar's lobus medius, together with one or more of the lateral group of cerebellar nuclei, namely, the dentatus, emboliformis and globosus. This however cannot be done at present with assurance because the story of the development of these lateral nuclei is not so fully known.

DISCUSSION

The following questions submitted to Dr. Larsell before the Commission, together with the answers to them, are here reported verbatim.

DR. LEWELLYS F. BARKER: I would like to ask Dr. Larsell if his studies permit him to take a position in regard to the relations of the pyramis; does he regard it as belonging to the posterior lobe or to the middle lobe?

DR. LARSELL: I have not arrived at that point yet.

DR. FREDERICK TILNEY: I would like to ask what significance you attach to the so-called paleo-cerebellum. As I understand it, you attribute to this portion of the cerebellum, the entire vestibular activity; that is in the higher vertebrates. Is this correct?

DR. LARSELL: I would say that the cerebellum has its origin in relation to two systems, namely, the central connections of the vestibular and lateral line system, on the one hand, and the spino-cerebellar and cerebral connections on the other hand. While other factors enter in, yet it appears to me that the region with which the vestibulo-lateral apparatus is connected should be considered the most ancient part of the cerebellum and rightly the paleocerebellum. Other structures grew up from that, as we begin to find in the reptiles, in which forms the lateralis system is absent and the vestibular apparatus is greatly reduced. It appears to me that a natural division between the old cerebellum and the new cerebellum, as found in mammals, is shown in the relative importance of the vestibulo-lateral connections in the aquatic forms, as compared with the spinal and cerebral connections. The two latter begin to assume a predominant place first in the reptiles. The vestibular parts of the cerebellum are retained in the reptiles, but in reduced condition, due perhaps to the close-to-the-ground method of locomotion of these animals. In birds and mammals the vestibular part of the cerebellum has developed from the ancestral reptilian type into a larger and more important structure, parallel with the greater demand, as compared with reptiles, on the vestibular apparatus in these forms. At the same time that part of the cerebellum which has spinal and cerebral connections is also assuming greater and greater functional importance, perhaps at an even more rapid rate. Those parts of the mammalian cerebellum which correspond morphologically to the vestibular and vestibulo-lateral cerebellum of lower vertebrates, possess predominantly, if not entirely, vestibular connections, hence my grouping them with the paleocerebellum.

DR. SMITH ELY JELLIFFE: It occurs to me that the "lateral-line moiety" is a content which Dr. Larsell drops out. May there not be some vestigial remnants of it up through the higher scales of animals, and if so, what vestigial remnants may be traceable in possible connection or possible cerebellar functions. This I believe Dr. Tilney is going to discuss later on. For instance, we know we have a vestigial gill slit left in mammals, and the thing that would interest me is to know if there are any traces of vestigial lateral line organs persisting.

DR. LARSELL: So far as I know, Dr. Jelliffe, there is nothing of the sort persisting in the nervous system of higher forms. There may be, but I have no evidence of it.

DR. TILNEY: Another point I would like to make is, in your studies, particularly of the selachians, have you observed any cells in the bulbar portion of the cerebellum which resemble in any way the Purkinje cells?

DR. LARSELL: In the elasmobranch they may be present. I have not personally studied the cerebellum of selachians to any great extent, but in the amphibia Purkinje cells are present in very primitive form, in the bulbar portion of the cerebellum.

DR. STEWART PATON: The life history of the individual in many respects is an interesting comparison with the history of the race. The oldest part of the nervous system begins at about the level of the seventh, eighth, ninth and tenth, cerebral nerves at a very early period and connections with the cerebellum exist.

I should like to ask why, at these very early stages before the ocular muscles function they should be connected with the cerebellum?

DR. LARSELL: The only suggestion I have to make is that the frog tadpole is not only an embryo but a functioning embryo; that is, an embryo that is using all its organs at the same time that it is also developing. Possibly the early connections of proprioceptive fibers from the eye-muscles, and the connections of the midbrain and other parts with the cerebellar region, is what we might consider a precocious development of these parts, due to some form of "besoin," if one may use a Lamarckian expression. I do not wish to emphasize the Lamarckian expression, but rather desire to call attention to the physiological needs of the functioning and active larva, which it seems to me would bring about early development of certain anatomical structures in the frog which in other forms may appear later. I do not know how early the ocular muscles begin to function in the tadpole, but other somatic muscles begin to respond to stimuli, at least in *Amblystoma*, at relatively earlier stages than those I have used in my work, as Coghill has shown. In the 15-mm. total length tadpoles of *Hyla*, the earliest stages I have used, the ocular muscles are present and presumably functional.

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EXPLANATION OF ABBREVIATIONS IN ILLUSTRATIONS

<i>am.ant.</i> , ampulla anterior	<i>n.VII</i> , nervus facialis
<i>am.post.</i> , ampulla posterior	<i>n.VII l.l.</i> , nervus lateralis anterior
<i>aq.S.</i> , aqueductus Sylvii	<i>n.VIII</i> , nervus acusticus
<i>c.ant.</i> , canalis anterior	<i>n.VIII d.</i> , nervus VIII dorsalis
<i>cb.</i> , cerebellum	<i>n.VIII v.</i> , nervus VIII ventralis
<i>cb.pl.</i> , cerebellar plate	<i>nod.</i> , nodulus
<i>c.c.</i> , canalis centralis	<i>nuc.d.m.</i> , nucleus dorso-medialis
<i>c.cb.</i> , corpus cerebelli	<i>nuc.V m.</i> , nucleus motorius V
<i>c.ext.</i> , canalis externa	<i>nuc.VII m.</i> , nucleus motorius VII
<i>con.l.l.l.</i> , conrescentia lobus lateralis	<i>nuc.cb.</i> , nucleus cerebelli
<i>c.post.</i> , canalis posterior	<i>nuc.d.mgc.</i> , nucleus dorsalis magnocellularis
<i>cr.cb.</i> , crista cerebelli	<i>nuc.isth.</i> , nucleus isthmi
<i>d.a.</i> , diverticulum anterior	<i>nuc.vest.</i> , nucleus vestibularis
<i>em.gr.</i> , eminentia granularis	<i>nuc.v.l.</i> , nucleus ventro-lateralis
<i>em.V</i> , eminentia trigemini	<i>p.ba.co.</i> , pars basilaris cochleae
<i>em.v.</i> , eminentia cerebellaris ventralis	<i>par.</i> , paraflocculus
<i>f.arc.int.</i> , fibrae arcuatae internae	<i>pl.ch.</i> , plexus chorioideus
<i>f.l.m.</i> , fasciculus longitudinalis medialis	<i>pyr.</i> , pyramis
<i>floc.</i> , flocculus	<i>r.l.</i> , recessus lateralis rhombencephali
<i>f.sol.</i> , fasciculus solitarius	<i>r.V</i> , sensory root of trigeminus
<i>gn.VII</i> , ganglion of facialis	<i>r.V sp.</i> , radix spinalis trigemini
<i>gn.vest.</i> , ganglion of vestibularis	<i>r.VII l.l.</i> , radix lateralis anterior
<i>hem.cb.</i> , cerebellar hemisphere	<i>r.VII l.l.d.</i> , radix lateralis anterior dorsalis
<i>l.aur.</i> , lobus auricularis	<i>r.VII l.l.m.</i> , radix lateralis anterior medialis
<i>ling.</i> , lingua	<i>r.VII l.l.v.</i> , radix lateralis anterior ventralis
<i>l.l.l.</i> , lobus lineae lateralis	<i>r.VIII</i> , radix acusticus
<i>lm.</i> , lemniscus	<i>r.VIII ant.</i> , radix anterior acusticus
<i>mes.</i> , mesencephalon	<i>r.VIII post.</i> , radix posterior acusticus
<i>m.obl.</i> , medulla oblongata	
<i>m.sp.</i> , medulla spinalis	
<i>n.V</i> , nervus trigemini	

- r.X ll.*, radix lateralis posterior
r.X ll.v., radix lateralis posterior ventralis
sac., sacculus
sac.ap., saccular appendage
s.a., stratum album
si.ut.sup., sinus utriculi superior
s.g., stratum griseum
s.gr., stratum granulare
s.l., sulcus limitans
s.mol., stratum molecularis
s.pur.c., stratum of Purkinje cells
s.v.cb., sulcus cerebellaris ventralis
tae.ch., taenia chorioidea
t.opt., tectum opticum
teg., tegmentum
tr.a., dorsal longitudinal tract of area acoustica
tr.b., ventral longitudinal tract of area acoustica
tr.b.t., tractus bulbo-tectalis
tr.sp.cb., tractus spino-cerebellaris
tr.sp.cb.v., tractus spinocerebellaris ventralis
tr.sp.t., tractus spino-tectalis
tr.sp.V., tractus trigemini-spinalis
tr.t.b., tractus tecto-bulbaris
tr.vest.aur., tractus vestibulo-auriculi.
tr.vest.cb., tractus vestibulo-cerebellaris
tr.vest.cb.d., tractus vestibulo-cerebellaris direct
uv., uvula
val.cb., valvula cerebelli
vent.IV, ventriculus quartus
vest.lat., lateral pouches of vestibule
v.m.a., velum medullare anterius

CHAPTER VIII

THE PHYLOGENY OF THE AFFERENT CEREBELLAR PATHWAYS

WILLIAM H. F. ADDISON, M.D.

THE aim of this report is to describe the phylogeny of the cerebellum by a consideration mainly of its afferent tracts. These tracts are of more diverse origin in fishes than in other classes of Vertebrates, so the fishes make a favorable starting point for the discussion of these tracts. The fishes, like all the lower aquatic animals, are characterized by the possession of a special set of sense-organs, the so-called lateral line organs. From these run lateral line nerves to the medulla oblongata, where they end mostly in distinct reception-nuclei, but partly in lateral areas cephalad of these.

The vestibular organs are developed equally early, and the vestibular nerves accompany certain of the lateral line nerves and have a similar destination. Whereas the lateral line system disappears entirely in animals above the amphibians, the vestibular system persists and retains its important functions.

From the reception-nuclei of the laterali-vestibular nerves, proceeds an important secondary tract, the tractus laterali-vestibulo-mesencephalicus (lemniscus lateralis of fishes) to the torus semi-circularis of the mid-brain. With the torus semi-circularis is closely related the nucleus lateralis valvulae, and from the latter runs a large and important though short tract, the tractus mesencephalo-cerebellaris posterior or tractus tegmento-cerebellaris, to the more median parts of the cerebellum—the corpus cerebelli. Of these two destinations of the laterali-vestibular impulses, the former (in the eminentiae granulares, cristae cerebellares, auricles) is to be considered the most primitive and the latter (in the corpus and valvula) a later derivative.

Into the corpus cerebelli at the same time come other important connections, of which one may mention first a tract from the roof of the mid-brain (tectum opticum) arising from its most cephalic part. This is the tractus mesencephalo-cerebellaris anterior or tractus tecto-cerebellaris and forms a connection between optic centers and the

cerebellum. This tract appears very early in phylogeny and has persisted throughout the vertebrate series, though in a diminished form, until the lowest mammals. It has been recently pointed out in *Ornithorhynchus paradoxus* (Marion Hines-Loeb) and in opossum. There is another tract arriving from a more frontal position, which is little understood, the tractus lobo-cerebellaris, from the hypothalamic structures which are so well developed in the fish, the lobi inferiores hypothalamici.

Even in these early stages there is another connection already present which persists and increases in importance as we ascend the vertebrate scale. This is derived from the spinal cord and bulb, and is the tractus spino- et olivo-cerebellaris. This olivary component is at first indefinite, corresponding to the slight development of the inferior-olivary nucleus. The spino-cerebellar tract assumes increasing size and importance and becomes the dorsal and ventral spino-cerebellar tracts of man, and when the olive becomes definitely established, there is a distinct tractus olivo-cerebellaris.

To these tracts seen in Teleosts there is added no new important pathway until we reach the Mammals, and there coincident with the great development of the neopallium, comes a new afferent connection, the cortico-ponto-cerebellar pathway.

The gross arrangement of the parts connected with the cerebellar functions is well illustrated in the primitive sharks, such as *Laemargus microcephalicus*. Into the auricles come the more direct laterali-vestibular impulses, and into the corpus cerebelli come the optic, spinal and indirect laterali-vestibular impulses. They together make up the more definite parts of the cerebellum. In a somewhat higher form, *Ceratodus*, a Dipnoan, or lung fish, the finer details have been recently worked out by van der Horst (1925). Here the auricles are in much closer relation to the caudal end of the corpus cerebelli, and as additional outlying parts of the laterali-vestibular systems are seen the eminentia granularis and the crista cerebellaris. Van der Horst deduces from his comparative anatomical researches that the size of the auricle is dependent upon the size of the dorsal lateralline nerves, and the size of the eminentia granularis upon the size of the ventral lateral line nerves and the vestibular nerves. Inasmuch as in Teleosts the lateral line nerves enter mostly in the ventral position, the auricle in Teleosts becomes greatly diminished and often is not present.

TABLE VI
AFFERENT CEREBELLAR PATHWAYS

	TR. VESTIBULO-C	TR. LATERALI-C	TR. MESEN-CEPHALO-C POSTERIOR OR TEGMENTO-C	TR. MESEN-CEPHALO-C ANTERIOR OR TECTO-C	TR. LOBO-C OR HYPOTHALAMO-C	TR. SPINO-ET OLIVO-C	CEREBRE-PONTO-C PATHWAY	TR. QUINTO-C
Cyclostomes.....	+	+	+	+	+	(?) Probably	0	+ Ceratodus
Sharks and rays..	+	+	+	+	+	+	0	+ Herrick
Teleosts.....	+	+	0	+	+ Very small	+	0	+ Larsell
Urodeles.....	+	+	0	+	0	+	0	+ Ingvar
Anura.....	+	+ Larva	0	+	0	+	0	
Reptiles.....	+	0	0	+	0	+	0	
Birds.....	+	0	0	+	0	+	0	
Mammals.....	+	0	0	+ Lowest 0 (?)	0	++	+	

So in Teleosts we have the spatial arrangements of the cerebellar parts in this manner—there is a basal region concerned with more direct laterali-vestibular impulses, and a medial part, the corpus, concerned with optic, hypothalamic, spinal and more indirect laterali-vestibular impulses. In Teleosts there is another cerebellar part, the valvula cerebelli, which is usually a small cephalic extension. This may be shown in a median sagittal section of *Gadus*. Now in this form there may be traced some fiber-bundles of the anterior lateral line nerves into the valvula, and also some fiber-bundles of the tractus mesencephalo-cerebellaris posterior, so that the valvula may be regarded as belonging primarily to the laterali-vestibular portion of the cerebellum. Thus in Teleosts, there are comprised in the laterali-vestibular portions the eminentiae granulares, cristae cerebellares and valvula, which together form a more or less continuous basal part, on which is the superadded corpus cerebelli. The Teleostean cerebellum is a highly specialized structure, showing in exaggerated form, the same component parts as the cerebellum of the urodele Amphibians.

When we come to the mature anuran Amphibians, which have become adapted for life on land, there is loss of the lateral line system, including its peripheral nerves and central connections, but persistence and increase of the vestibular system. In connection with the greater development of the paired limbs there is great development of the spinal connections in the spino-cerebellar tracts. There is also loss of the hypothalamic connection, but persistence of the optic connections. There are two main portions, the median bilaterally formed corpus, and the lateral areas—the representatives of the auricles and eminentiae granulares. The lateral areas receive the vestibular fibers, the median corpus all the other tracts.

The cerebella of reptiles and birds are of the same fundamental pattern as in the anuran Amphibians. The vestibular tracts are associated with the more definite projecting masses, the flocculi, which are lateral structures closely associated with the caudal region of the corpus cerebelli.

Throughout the vertebrate series, no new definite tract is added to the afferent cerebellar pathways until in the mammals there appears the cortico-ponto-cerebellar pathway, and this becomes very important as we ascend the mammalian scale. At the same time the inferior olivary nucleus becomes more and more developed so that we readily recognize separate olivo-cerebellar and spino-cerebellar pathways.

The vestibulo-cerebellar tracts remain, but the tecto-cerebellar tracts have been identified only in the most primitive mammals. There is still some debate about the quinto-cerebellar tract. Thus there are four well-developed pathways in mammals, coming from spinal cord, inferior olive, vestibular apparatus, and cerebral cortex, by way of the pontile nuclei.

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CHAPTER IX

A COMPARATIVE QUANTITATIVE STUDY IN PROPRIOCEPTIVE TRACTS OF MAMMALS¹

ARTHUR WEIL, M.D.

THE present paper is based on the study of serial sections of brains of different mammals stained with the Weigert-Pal method. Its purpose is to show the quantitative relationship of both cerebellar and cerebral afferent pathways for proprioceptive impulses. In man, these are the spino-cerebellar tracts and the posterior spinal columns. These tracts have been compared with corresponding anatomical structures in different mammals. Finally the restiform body, as the main collective pathway of proprioceptive afferents to the cerebellum, and the pyramidal tracts have been compared.

In mammals there are two spino-cerebellar tracts: The posterior (Flechsig's) originates in the spinal nucleus dorsalis (Clarke's Column) from L-I to C-VIII. According to Bing (1) it originates further down (L-II-III) in man and at the lower end of the lumbar cord in tailed animals. Its fibers do not cross within the spinal cord. They enter the cerebellum through the restiform body and pass to the posterior and anterior portions of the vermis of the same and opposite sides (Lobus centralis, culmen, lobus posterior and lobus pyramidalis). Some of the fibers go to the nucleus fastigii. The relation of the number of crossing fibers to non-crossing fibers in apes is according to MacNalty and Horsley, 1:2.

The anterior (Gowers') spino-cerebellar tract originates in ganglion cells of the dorsal horn from L-III-IV up to the upper cervical region. Its fibers cross in the ventral commissure of the spinal cord and pass ventrally to the posterior tract. They go farther frontal than the posterior part entering the cerebellum in the region of the brachium conjunctivum anterius. They end mainly in the lobulus centralis and the culmen; a few of the fibers go to the pyramis and the nucleus fastigii of the same side. The relation of crossed to uncrossed fibers

¹ From the Neuropathology Laboratory, Montefiore Hospital, New York.

in anthropoids is 1:4 (2). According to Bing there is a total crossing in man and most of the fibers pass to the anterior-posterior part of the vermis, while the posterior spino-cerebellar tract passes mainly into the anterior superior part of the vermis. The anterior-inferior part of the vermis, namely lobulus centralis and culmen, therefore receives fibers from both tracts, while the pyramis is mainly supplied by the posterior spino-cerebellar tract. From this kind of distribution it may be concluded that both anterior and posterior spino-cerebellar tracts conduct impulses from all parts of the body, and that both lower and upper extremities are represented in both tracts. From an anatomical study of a case of transverse myelitis with destruction of the gray matter of the spinal cord up to D-VI, it appears that the fibers of the cervical segments pass mainly into the posterior spino-cerebellar tract. This may be seen from the planimetric index, which is less for the degenerated fibers of the anterior tract at C-VII as compared to C-II (8.8 and 4.2), while the index for the degenerated fibers of the posterior tract is more at C-VII (7.5) than at C-II (6.5), indicating that the ascending degenerated fibers of the posterior spino-cerebellar tract are pushed ventrally by new incoming fibers of the cervical segments.

In order to compare the quantitative estimations of the spino-cerebellar tracts to those of other pathways, the author followed a suggestion made by Tilney and calculated the planimetric index of different tracts. These are well outlined and may easily be measured with the planimeter. For this purpose the restiform body was chosen before it enters the cerebellum, the posterior columns just before the formation of the posterior nuclei and the pyramidal tracts at the same level as the restiform body. The figures so obtained were assembled in a table and converted into a curve. The figures for the anterior and posterior spino-cerebellar tracts are naturally not exact, because those tracts are not very well defined in Pal-Weigert preparations. In the human sections they are nearer the real value because they were measured in a case of descending pyramidal tract degeneration.

The technic of the calculation of the planimetric index consists of the following steps: (1) enlargements of the sections with a photographic lense fifteen to twenty times. (2) Drawing of the contours of the section, of the outlines of the tracts and of the middle line. (3) Measuring the area of the plane covered by half of the section and the area of the plane covered by the tracts to be measured by means

TABLE VII
PLANIMETRIC INDEX

SECTION	TRACTS	KANGAROO	GIRAFFE	TAPIR	HORSE	RABBIT	CAT	TARSUS	GIBBON	GORILLA	CHIMPANZEE	MAN
Medulla oblongata at and below decussation of the pyramids	Posterior spino-cerebellar							3.4	4.0			8.3
	Anterior spino-cerebellar							1.6	1.9			4.2
	Posterior and anterior spino-cerebellar		5.2		4.1			5.0	5.9	4.2	6.1	12.5
	Posterior columns	15.3	11.0	13.3	15.5	11.7	15.2	14.4	23.6	26.8	28.6	29.2
Medulla oblongata at caudal end of inferior olives	Posterior spino-cerebellar	3.0		6.2					3.7		4.6	
	Anterior spino-cerebellar	2.1		2.6					1.6		2.0	
	Posterior and anterior spino-cerebellar	5.1		8.8	8.9		7.6		5.3	4.8	6.6	8.2
	Pyramids	4.8	3.0	4.1	3.4	3.3	8.3	7.7	11.1	11.3	10.4	10.2
Middle of inferior olives	Restiform body	7.6	11.4	10.4	13.2	5.1	8.0	6.4	5.9	6.7	5.8	9.9

of a planimeter. (4) Multiplying the numbers of square inches (or square centimeters) of the area of the tract by 100 and dividing by the number of square inches (or square centimeters) obtained for the area of half a section. The result represents the percentage relation of the size of the plane covered by a given tract to the size of the plane covered by the corresponding half of the section.

Table VII gives the results obtained for different mammals. Table VIII shows the relation of the areas of the posterior columns to those of the restiform body and of the areas of the posterior columns to

TABLE VIII
RELATION OF PLANIMETRIC INDICES

	POSTERIOR COLUMNS: RESTIFORM BODY	POSTERIOR COLUMNS: PYRAMIDS
Kangaroo.....	15.3 : 7.6 = 2.0 : 1	15.3 : 4.8 = 3.2 : 1
Giraffe.....	11.0 : 11.4 = 1.0 : 1	11.0 : 3.0 = 3.7 : 1
Tapir.....	13.3 : 10.4 = 1.3 : 1	13.3 : 4.1 = 3.3 : 1
Horse.....	15.5 : 13.2 = 1.2 : 1	15.5 : 3.4 = 4.6 : 1
Rabbit.....	11.7 : 5.1 = 2.3 : 1	11.7 : 3.3 = 3.5 : 1
Cat.....	15.2 : 8.0 = 1.9 : 1	15.2 : 8.3 = 1.8 : 1
Tarsius.....	14.4 : 6.4 = 2.2 : 1	14.4 : 7.7 = 1.9 : 1
Gibbon.....	23.6 : 5.9 = 4.0 : 1	23.6 : 11.1 = 2.1 : 1
Gorilla.....	26.8 : 6.7 = 4.0 : 1	26.8 : 12.3 = 2.4 : 1
Chimpanzee.....	28.6 : 5.8 = 4.9 : 1	28.6 : 10.4 = 2.7 : 1
Man.....	29.2 : 9.9 = 3.0 : 1	29.2 : 10.2 = 2.9 : 1

those of the pyramidal tracts. Figure 112 represents the main results of table VII graphically, figure 113 the results of table VIII.

A study of the tables and figures shows that within a given mammalian order there is a well defined constant relationship between the different pathways which were investigated. The relation of the posterior spino-cerebellar tracts to the anterior in anthropoids is approximately 2:1. The preponderance of the restiform body in ungulates is evident. The carnivora and lower primates show an intermediary stage: the pyramidal tracts are relatively more increased than the posterior columns as compared with the preceding

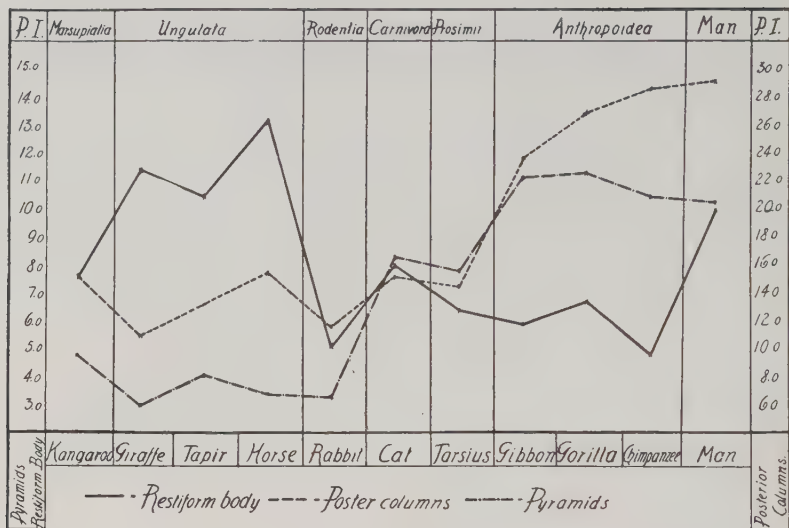


FIG. 112. Planimetric indices. The numbers of the left ordinate indicate planimetric indices of pyramids and restiform body; those of the right ordinate indicate the planimetric index of the posterior columns.

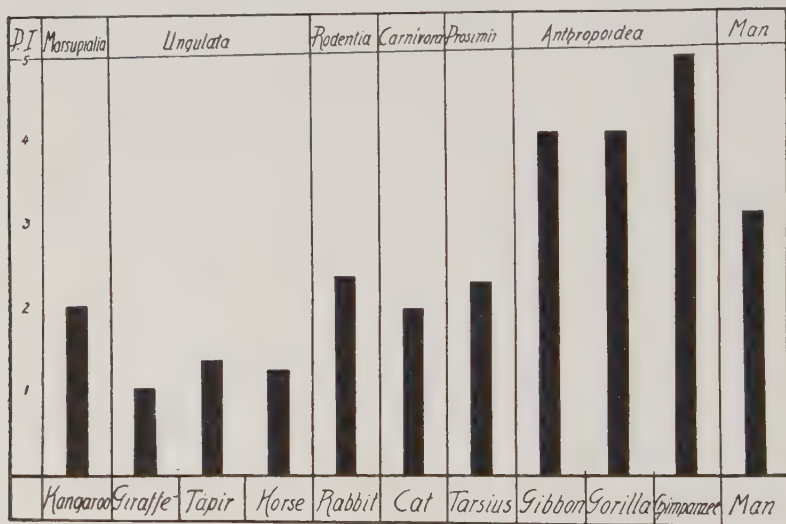


FIG. 113. Posterior columns and restiform body. The black columns indicate how many times the planimetric index of the posterior columns is larger than that of the restiform body.

orders. The increase of the relative size of pyramids and posterior columns from ungulates to anthropoids and man is nearly parallel for both of the tracts. Only in gorilla, chimpanzee and man does the planimetric index of the posterior columns increase relatively more than the index of the pyramidal tracts. The latter remain nearly constant throughout the order of the higher primates. The index for the restiform body is nearly the same in marsupials, rodents, carnivores and primates. Only in ungulates and to a lesser degree in man does this index rise above the average.

It is tempting to attempt to correlate these anatomical findings with the physiological behavior of a given species. The preponderance of cerebellar afferents in ungulates may be related to their speed, which requires great exactness in muscular synergy. The increase of the pyramidal tracts and posterior columns in higher primates may be related to their skill in performing complicated voluntary movements, while the cerebellar functions remain in the same level as in the other mammals, the ungulates excepted.

Only one well-established conclusion may be drawn: The planimetric indices which were studied show the preponderance of cerebellar afferents in ungulates, the preponderance of cerebral afferents in higher primates. Or in phylogenetic terms:

Spino-cerebral afferents and cerebro-spinal efferents increase with the mammalian ascendance, while spino-cerebellar afferents remain relatively constant.

I wish to express my thanks to Dr. F. Tilney who put his collection of serial sections of mammalian brains at my disposal.

DISCUSSION

The following question submitted to Dr. Weil before the Commission, together with the answers to them, are here reported verbatim.

PRESIDENT FREDERICK TILNEY: Are the different fibers within the spino-cerebellar tracts arranged according to their segmental origin?

DR. ARTHUR WEIL: The lantern slide from the case of transverse myelitis shows that the degenerated area in C-II was at the periphery of the spinal cord. In other words, the fibers which come from the upper lumbar and lower dorsal segments are arranged at the periphery, more outward than the fibers from higher segments. The posterior part of Flechsig's tract in higher cervical segments of the same case did not show degeneration of myelin sheaths, this would imply the

conclusion that fibers joining this tract above the lesion were arranged more posteriorly than the lumbar and lower dorsal fibers.

DR. TILNEY: We know that the restiform body is a complex afferent system to the cerebellum. We know that it contains fibers coming from the cord and also fibers coming from the olive, which occupy what is generally known as the core-bundle. I would like to ask whether the planimetric index of the restiform body, as compared with the index of the posterior spino-cerebellar tract, will allow of any conclusions as to the part that the olivo-cerebellar fibers play in the inferior cerebellar peduncle? The point being, can you give us any idea of the percentage of contribution which comes from the olive, in a phyletic way, and that which comes from the spinal cord?

DR. WEIL: Theoretically, if we deduct the planimetric index of the posterior spino-cerebellar tract from the restiform body, we should find the difference to be the rest of the afferent pathways, *i.e.*, mainly olivo-cerebellar fibers. If we apply this method to ungulates we find, that apparently a larger number of olivo-cerebellar fibers (planimetric index in tapir 4.2) enters the cerebellum than in other mammals (3.0 in cat, 1.2 in chimpanzee). In studying the ungulate sections more closely we find, that in the more cranial sections through the restiform body the inferior olives have disappeared, and that only a few olivo-cerebellar fibers enter at this level. We have to conclude that in ungulates the part of fibers in the restiform body—other than posterior-spino-cerebellar and olivo-cerebellar—is much larger than in other mammals (fibers from the nuclei of the posterior funiculi, from the nuclei of the lateral columns?). In man the olivo-cerebellar fibers form between 40 and 50 per cent of the restiform body.

DR. STEWART PATON: Mr. Chairman, in connection with this very interesting paper, I should like to indicate an interesting field of research. In the chick at six and a half days the embryo responds to electrical stimuli; it also responds to changes in position. At that period there are neuro fibrils between the levels of the third and vagus nerves. The posterior longitudinal fasciculus, as Vogt and Kappers have shown, is one of the very oldest tracts. At this time, the semicircular canals possibly play a very interesting rôle in connection with the stabilizing reactions.

Connections exist at this time with the cerebellum, but I don't wish to give the details as I am still conducting the investigations.

The thyroid and adrenals have already received bundles of neuro fibrils. Probably the first endocrine organ to become functionally active is the thyroid, followed closely by the suprarenals.

DR. ADOLF MEYER: Have you had any opportunity to investigate Clarke's column and the other contributing cells of the spinal segments for the origin of the spino-cerebellar tracts?

DR. WEIL: My main attention was concentrated on the tracts themselves and I only can cite references from literature about this point. It seems that phylo-

genetically the cells which contribute to the origin of the spino-cerebellar tracts have a more dorsal position in amphibia than Clarke's columns in mammals. Sala could show in tadpoles that the large cells which form the posterior horns of the gray matter of the spinal cord project fibers to the lateral part of the lateral funiculi to a field which corresponds later to the spino-cerebellar tract.

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Section II

PHYSIOLOGICAL AND EXPERIMENTAL
INVESTIGATION OF THE
CEREBELLUM

CHAPTER X

THE STATIC SYSTEM AND ITS RELATION TO CEREBELLAR FUNCTION

J. RAMSAY HUNT, M.D.

WHEN the cerebellum is being considered from various aspects, it may be of interest to present a conception of its function, as an organ for the control of *posture synergy*; a function of motility which, I believe, is quite distinct from that of movement.

It has long been recognized that the afferent pathways originate in highly specialized end organs and subserve specific forms of sensibility. And these various groups of sensory function, touch, pain, temperature and deep sensibility, are anatomically and physiologically quite distinct.

The efferent system, on the other hand, has been regarded as a single physiological pathway, whose function is the control of the activities of voluntary and involuntary muscle, notwithstanding a great mass of evidence from various fields of research, indicating the dual nature of the peripheral motor mechanism.

STATIC AND KINETIC SYSTEMS

In my presidential address to The American Neurological Association in 1920 (1), the efferent nervous system was presented from a new point of view. In this conception, the various neural pathways subserving motility were divided into two great systems, which are anatomically and physiologically quite distinct. One of these was termed the *kinetic system*, and was identified with the function of movement; while the other, the *static system*, was related to the function of posture. It was held that the nerve impulses producing motion and those maintaining posture were different in character, and traversed their own physiological systems, as is the case with the different modalities of sensory function.

When one considers the relations of the organism to the outer world, the wisdom of such a division of motility is obvious. One function of the motor pathway is the maintenance of the postural fixation of

muscles, which tends to counteract the static forces of gravity and atmospheric pressure, while the other function is motional, by which the organism is enabled to change its position in space. *Kinesis*, therefore is dependent upon the active contractility of the muscle fiber while *stasis* is that more passive form of muscle function which we recognize in posture, attitude and equilibrium. The harmonious coöperation of these two types of function underlies the muscular activities of all organic life, a relation which is so intimate that the independence of the two underlying systems is only revealed by the dissociations of disease: a dissociation of motility, comparable to dissociations of sensibility in the afferent sphere.

The importance of this to our present discussion is the relation which the cerebellum bears to the posturing function of muscles, for in my conception of the efferent pathways, the cerebellum is to be regarded as the chief ganglion of the static or posture system of motility.

It would carry us too far afield at this time to give in all its details my conception of the static and kinetic systems, their function and symptomatology and the great array of evidence on which the hypothesis rests. For this evidence and the literature of the subject I must refer to my previously published articles on this subject (2).

I would, however, state that in the sphere of movement *archeo-kinetic*, *paleo-kinetic* and *neo-kinetic* systems are recognized, representing reflex, automatic-associated and dissociated types of movement, and which correspond anatomically to the segmental, the strio-spinal and the cortico-spinal systems of motility.

A similar division of function may also be recognized in the posture sphere, *archeo-static*, *paleo-static* and *neo-static* systems, subserving the corresponding functions of postural activity. The *archeo-static* systems are represented in the segmental mechanism of the spinal cord and brain stem, and here I would emphasize the important experimental researches of R. Magnus (3) on posture reflexes and the localization of posture mechanisms in the brain stem and spinal cord.

The other static functions are represented by the cortico-cerebellar and cerebello-spinal systems. The *paleo-cerebellum* subserving the older types of postural synergy, while the *neo-cerebellum* through its connections with the pallium furnishes the postural elements of *neokinesis*. In the static system the fronto-ponto-cerebellar tract may be regarded as the homologue of the pyramidal tracts in the kinetic

sphere. Both of these pathways are of late development in the phylogenetic sense and both receive their myelin sheaths subsequent to birth.

It is, therefore, through the cortico-cerebello-spinal pathways of the static system that the various types of movement receive their postural tone and synergy, through the mediation of its chief ganglion the cerebellum.

It is interesting to observe that all the posture systems, neostatic as well as paleostatic, pass to the cerebellum for final intergration, which is in harmony with the nature of the posturing mechanism and its unconscious rôle in motility. For while the higher forms of movement are initiated as conscious and voluntary processes, the corresponding postures are secondary and follow automatically in the path of movement. It is for this reason, I believe, that the neostatic system, which is the homologue of the pyramidal system, does not pass directly to the gray columns of the spinal cord, but is directed first to the cerebellum, which is the great central correlating mechanism for posture function.

RELATION OF THE DUAL SYSTEM OF MOTILITY TO SYMPTOMATOLOGY

When the motor pathways are injured or diseased it may be stated as a general principle of symptomatology that a lesion of the kinetic system causes a disorder of movement and of the static system a disorder of posture.

In the varied symptomatology of motor disorders, such manifestations as fibrillary twitchings, myokymia, myoclonus, chorea, clonus and tremor are related to the kinetic system. While such disorders as myotonia, catatonia and the cerebellar syndrome are related to the static system.

STATESTHETIC AND KINESTHETIC SYSTEMS

In the sensory sphere the sense of movement and the sense of posture are well recognized components of deep sensibility. In my previous study I have presented the evidence in favor of the existence of *statesthetic* and *kinesthetic* divisions of the proprioceptive system. A disorder of the kinesthetic system produces a loss of the sense of movement—a kinetic ataxia, while a disorder of the statesthetic system produces a loss of postural sensibility—a static ataxia. The statesthetic system is the sensory component underlying plastic tonus (statotonus), the “lengthening and shortening reactions” of

muscles and other manifestations of postural tone, *e.g.*, reflexes of posture. The kinesthetic system, on the other hand, is the sensory component underlying the "twitch," the contractile tonus (kinetotonus) and reflexes of movement.

In disease, these two functions of the proprioceptive system are usually involved together and frequently in the same degree. In some cases, *e.g.*, in tabes, a more selective involvement may occur, causing ataxia, loss of tendon reflexes, with little or no loss of postural tone; on the other hand, there may be well marked hypotonia without ataxia or loss of tendon reflexes.

In the vestibular mechanism which is so closely related to the proprioceptive system a similar division is recognized and recent investigators, Magnus (4) and Barany (5) have shown the existence of a kinetic labyrinth, in which the semi-circular canals yield kinetic impulses and the statoliths static impressions in the regulation of movement and posture.

THE NEURO-MUSCULAR MECHANISM

Of even greater importance to our theory are certain structural and functional peculiarities of the neuro-muscular apparatus, for here we find the clearest evidence of that duality of efferent function which I conceive as existing at all levels of the nervous system. It is at this level that Mosso (7), Grützner (8) and Botazzi (9), and Sherrington (10) laid the foundation for this conception by their work on the motor functions of the vegetative and reflex nervous systems.

A very striking illustration of the dual nature of muscle function may be observed in certain of the invertebrates. In bivalved mollusks closure of the shell is effected by the contraction of two distinct muscles, a contractile muscle which is striated, and an arrest muscle which is nonstriated. The rapid movement of closure of the shell is produced by the striated muscle. This is accompanied by a slower contraction of the arrest muscle which becomes fixed as soon as the movement ceases. The arrest muscle thus fixes in posture the closing movement of the shell, which is then able to withstand an enormous degree of pressure before relaxation is induced. A similar division of movement and posturing muscles may also be observed in *Echinus* and *Pecten* and these muscles have separate and distinct sources of innervation.

It is also of interest to note that in the vegetable world the existence

of a separate contractile and statolithic mechanisms have been demonstrated by Sir Jagadie Bose (6) in his investigation of the motor activities of plants.

All contractile tissue as represented by the muscle fiber is composed of two substances which are histologically and physiologically quite distinct. One is the contractile substance, which in non-striated muscle consists of longitudinal fibrillae and in the striated muscle fiber is represented by the characteristic disc mechanism. This contractile mechanism, in terms of the physiologist, furnishes the twitch component of muscle function which in a larger sense is the movement of the muscle mass. It is generally estimated that the sarcostyles constitute from $\frac{1}{6}$ to $\frac{1}{2}$ of the total muscle mass.

The other component of the muscle fiber is the sarcoplasm which is a constituent of both striated and non-striated muscle, and which, according to many physiologists, furnishes a kind of postural tone to the contracting muscle fibers. The well known "lengthening and shortening" reaction is dependent upon this function of the sarcoplasm. By its means a muscle may be lengthened or shortened during contraction without corresponding changes in tension, which facilitates the easy transition from posture to movement which is so characteristic of motility.

To explain this lengthening and shortening reaction, Grützner postulates the existence of an internal fixation or check mechanism which he likens to a catch and ratchet mechanism by means of which the contractile cell may be fixed in any length.

The postural function of muscle was also shown to exist in the muscle of the batrachian heart by Botazzi. This author reached the conclusion that the motor activity of the heart muscle consists of two components, one the beat which is referred to the fibrillary or disk system and the other a tonic wave or oscillation of sarcoplasmic origin.

Von Uexküll (11) has also furnished very strong experimental evidence of the differences of function of these two components of the muscle fiber. He has shown that there are two kinds of fixation or *sperrung* of the muscle fiber, one a maximal fixation and the other a gliding fixation. Maximal fixation implies the utilization of the whole fixation power of the muscle. Gliding fixation, on the other hand, signifies the existence of various degrees and gradations of *sperrung* and would correspond to the varying shades and differences of muscular contraction which characterize the higher function of skeletal muscles.

The skeletal muscles, therefore, are capable not only of gradations of contractile function, but also of postural function, both of which would be necessary for the performance of the finer and more intricate manifestations of motility.

In this conception of internal fixation, Von Uexküll believes that the sarcoplasmic substance of the muscle fiber is converted into a mechanical posture apparatus by the conversion of sol into gel and a reconversion of gel to sol. This mechanism of fixation would, therefore, require not only clotting but also unclotting of the sarcoplasmic contents of the muscle cell.

Langelaan (12) and Sherrington (13) have also presented evidence showing that muscle tone consists of two components, a contractile and a plastic tone which is also in harmony with this conception. And a further confirmation comes from the chemical side (Pekelharing) (14), which tends to show certain differences in the chemistry of actively contracting and passively posturing muscle.

Here then is striking evidence from the field of biological research of the existence of separated myokinetic and myostatic mechanisms subserving respectively the functions of motion and posture.

In this connection it will also be recalled that the histologists, Perroncito (15) and Boeke (16) both demonstrated a dual innervation of the striated muscle fiber, the contractile mechanism being innervated by medullated and the sarcoplasm by a non-medullated nerve fiber. The plastic component of tonus, according to Boeke, is controlled by non-medullated nerve fiber, and the contractile component is under the control of the motor cell of the anterior horn.

Another striking confirmation of a dual efferent system is to be found in the researches of Kure, Hiramatsu and Naito (15), on the innervation of the diaphragm. These investigators were able to show by animal experimentation that the phrenic nerve conveys the kinetic impulses for this important muscle, while its tonus is received through the splanchnic system of the sympathetic. If the phrenic nerve is cut, the diaphragm is paralyzed but tonus is preserved. When the sympathetic nerve is cut, tonus is lost but motility is unaffected. As the diaphragm performs a relatively simple function it is not surprising that these two systems are dissociated and, as had already been shown by the experiments of Boeke, the same is true for the kinetic and static systems of the ocular muscles.

So that the results of histological investigation confirm those of

physiology on this important question of the dual function of the muscle fiber.

RELATION OF THE CEREBELLUM TO SYMPTOMATOLOGY

Let us now consider the cerebellum in its relation to symptomatology and I would here recall an experiment cited by André-Thomas (18) and also mentioned by Luciani (19); it is that of a dog whose cerebellum had been removed and which was unable to stand or walk, and yet when thrown into water could swim without difficulty.

This peculiar phenomenon and its explanation have, I believe, an important bearing on our theory. When the dog, without a cerebellum, attempts to stand or walk, posture synergy so essential to coördinated movement, is lacking and the animal crumples to the ground in response to the laws of gravity. In a supporting fluid like water, however, posture synergy is of secondary importance and the kinetic system with its synergies are intact, the act of swimming takes place without appreciable difficulty. It is, I believe, not unlikely that some of the cerebellar symptoms in human beings would disappear under similar conditions, although I know of no experiments covering this point.

In many respects the theory of a *stato-synergic function* of the cerebellum harmonizes with our modern conceptions of cerebellar symptomatology.

In the pioneer work of Luciani, it will be recalled that astasia together with atonia and asthenia formed his famous triad of symptoms, all of which today are recognized as constituents of the cerebellar syndrome.

Babinski's (20) more elaborate clinical analyses added greatly to our knowledge of cerebellar symptomatology but threw very little light on its more intimate relations to motility.

With the increase in our clinical knowledge, as a result of Babinski's brilliant contributions, an effort was made to unite the various manifestations of cerebellar disorder under a single syndrome and there followed Mill's and Weisenberg's conception of synergia as the essential function of the cerebellum.

André-Thomas, moved by the same tendency to find the underlying principle of the cerebellar syndrome, reduced all cerebellar phenomena to a *sthenic* function—a hypersthenia and hyposthenia of agonistic and antagonistic muscles.

Tilney's (22) conception is also concerned with synergia, in which the unit of synergy is composed of agonists and antagonists under the control of a dominant and check mechanism.

Ingvar (23), whose conception in some respects is similar to my own, regards the cerebellum as an organ for the regulation of the static and dynamic equilibrium of the body masses.

CEREBELLAR SYMPTOMS AND THE STATIC SYSTEM

Like these, more recent students of cerebellar function, I too would reduce its manifestations to a single essential syndrome, namely, the regulation of posture and postural tone. For I believe that loss of posture-energy is the cause of the scanning speech, cerebellar ataxia, intention tremor, hypermetria, adiadokokinesis and the nystagmus, which are characteristic of cerebellar disease.

In cerebellar ataxia, for example, a characteristic feature is the decomposition of movement which takes place during the execution of a coördinated act. When this is present it requires several disjointed movements to accomplish what is normally performed as a continuous one. This discontinuity of movement I would refer primarily to a disorder of posture coördination, which prevents the posture and motion systems from acting together in harmony. The decomposition is therefore a replacement manifestation in an effort to compensate for a defect in the posturing mechanism. In other words, it is a dissociated disturbance of motility due to loss of static synergy.

Hypermetria and dysmetria of cerebellar origin may also be explained by a failure of the posture system in its function of guiding and checking movement. For postural fixation and relaxation, in their various gradations, play an important rôle in regulating the exactness and niceties of movement. Especially is this true of starting and checking movements but also movement itself. For during movement there is a changing postural tone and synergy which is the secondary and unconscious factor in motility. The unconscious rôle of the posturing function is, I believe, largely responsible for its neglect as an important component of motility. For in any coördinated act *posture patterns* are a necessary complement of *motion patterns* and play an important rôle in giving stability and direction as well as in initiating and checking movement.

Adiadokokinesis may likewise be ascribed to a disorder of this

static function. The slowing of the quick succession movements which characterize this disorder is also dependent upon a diminution of the finer adjustments of fixation and release of the posture mechanism, which is necessary to the precise performance of such an act.

Perhaps the most striking disorder of this posturing mechanism is the cerebellar or intention tremor. This is a coarse ataxic oscillation which takes place during the passage of a movement. It is particularly at the end of the movement when the extremity tends to become fixed in posture that the intention tremor is usually most active.

Cerebellar nystagmus may also be mentioned as representing a similar mechanism. Here again the rhythmical movements of the eyeballs tend to increase when the attempt is made to fix the eyes in posture. And the same loss of the postural element I believe underlies such symptoms as the pendular knee jerk and the rebound phenomenon of Stewart and Holmes.

Therefore, while a certain gross motility disorder, the asynergia may be regarded as the fundamental symptom of cerebellar disease, I would limit this conception to one of posture asynergia, thus recognizing the essential relation of the cerebellum to the static system and its rôle in stato-synergy.

The importance of posture as a factor in motility should be emphasized because of the prevailing view, that the cerebellum controls the synergies of movements, for in a broad practical sense this is true. A paralysis of the postural component does produce a marked disorder of movement, but in a strict physiological sense, this is secondary and movement synergies are only impaired because of defects in the posture sphere.

In locomotor ataxia, for example, there is a serious disturbance of motility but this we recognize as secondary to a defect in the proprioceptive system on the afferent side.

In the same sense, a cerebellar ataxia also represents a serious disturbance of motility, but this too is only secondary to a defect in the static sphere.

Dissociation of motility is, therefore, an important factor in the realm of the efferent nervous system and when the cerebellum or the static system is the seat of disease the dissociated nature of the resulting disorder should be recognized even though motility in a general sense shows a disturbance. It is a more exact interpretation of the phenomena and is in harmony with our efforts to unravel the finer structure and functions of the nervous system.

DISCUSSION

The following questions submitted to Dr. Hunt before the Commission, together with the answers to them, are here reported verbatim.

DR. CHARLES K. MILLS: I would like to ask Dr. Hunt one or two simple questions. I think we all know what we mean by posture. The position which is taken by a skillful fencer is certainly a fine illustration, at least, to my mind, of posturing, but (and this is the question I would like to put before Dr. Hunt) is not the posturing which is accomplished in this way unquestionably the result of the exercise of kinetic energy? A skillful fencer learns to stand in a certain position. Standing in that position, he uses his musculature kinetically, if I may so use the term. He stands, taking a certain position of his head, to his trunk, arms and legs, which position is due to the synergic action of harmony of movement between these different parts.

I must confess I don't know much about the intimate nature of sarcoplasm, but I do know that kinetic energy is always used in all sorts of postures.

DR. J. RAMSAY HUNT: Dr. Mills asks a very pertinent question, and gives me an opportunity to explain what perhaps I did not make clear. Consider for a moment the question of sensation and the various components underlying general sensibility. In presenting one of the sensory systems, for instance, pain sensibility, it is entirely artificial to speak of it as we understand it in the strict neurological sense, as a perfectly separate and distinct modality of sensory function. It is really only a part of the great function of sensibility and is intimately connected, structurally as well as functionally, with all other systems of the great afferent pathway. And these various sensory systems all participate in what we recognize as sensibility.

I believe that a similar principle underlies motility and that this general function may be subdivided into two separate and distinct modalities of function—one *kinetic*, subserving movement, and the other *static*, subserving posture. While in both of these functions there are neural impulses and corresponding changes in the muscle mass the essential element of the striated mechanism is twitch or movement, while the essential element of the sarcoplasm is fixation or hardening of the muscle fiber or mass which produces a posture. The term kinetic is a descriptive one and indicates the relation of this system to movement and does not exclude the static system from also participating in movement, and the reverse is also true that the kinetic system participates in the function of posturing. They are mutually cooperative and not as Dr. Mills would infer mutually exclusive.

Of course it is a little difficult, after we have thought of the motor pathway always as a single physiological system to conceive it in terms of the cleavage which I have given, because such a division is artificial, it is created by the mind of man; it is simply a way we have of understanding and interpreting phenomena—but this is so in all science. What does nature know of atoms and electrons? But they mean something to us.

These functions of motion and posture as I conceive them are combined. They are mutually cooperating and to some extent also mutually antagonistic, because

if you are in a state of posture, something must be done to that posture before you move, and when you are in a state of movement, something must be done to that movement before you are in a state of posture, and such interaction is going on all the time. As a matter of fact, much more of our time is spent in posture than in movement, and it would seem as if nature in her wisdom had developed this function of posture which operates at a much lower level of energy dissipation than does the kinetic system. Furthermore, they are mutually strengthening to one another; they are mutually helpful. In every movement, the posture system plays a rôle and in every posture there is also a participation of the kinetic mechanism.

For example, Dr. Mills as a fencer would be in a sorry position if he had only his kinetic system because he couldn't posture with assurance. He would be in a still sorrier position if he had no kinetic system, because he would then have only posture and couldn't move and his antagonist would thrust him through. But if you could conceive of an intimate and beautiful adjustment of these two functions operating through separate, distinct motor systems then not only would the fencer posture but he could also move from one posture to another by a series of movements, and so on through all the changing vicissitudes of combat.

The evidence in favor of a posturing mechanism in muscles is very large, but this evidence happens to be in outlying fields of biological science, and we all know by experience how slow these are in being organized in our medical conceptions. There are many things that may have to be modified in my conception, but as a working hypothesis, to students of the cerebellar function, it will, I believe, have value.

DR. MILLS: No, I am satisfied that he has not explained the thing to my satisfaction, and I do not think he can; I mean, along the lines which he has taken. Position, or posture, after all, is the result of kinetic energy, of synergic movements. It is, and must always be. I do not doubt that there may be afferent impulses from the sympathetic, as well as from the somatic nervous system, but it does seem to me that it is simply playing with terms to speak of posture as something absolutely distinct and separate from synergic movement. I do not comprehend the necessity of the cleavage of the nervous apparatus into two parts, one for movements and the other for posture.

DR. HUNT: In the sensory sphere we recognize special end organs for touch and for pain and for temperature. We also recognize separate neurons and fiber systems in connection with these nerve endings. Now, whether we accept it or not, the proof is almost overwhelming in favor of muscle-fibers, both striated and non-striated, being composed of two very distinct mechanisms, which physiologically show quite distinct functions. Histologically they have proved two separate innervations for the striated muscle-fibers.

Now, is it logical to assume that neuro-muscular end organs which show duality of structure and function should not have corresponding central representations? I am sure that Dr. Mills does not find it difficult to accept cleavage in the afferent system in terms of pain and temperature sensibility; why then is it so difficult, providing the evidence is produced, to accept such a principle in the efferent sphere?

DR. STEWART PATON: More than 12 years ago I called attention to the first movement of the embryo, in response to stimulation, an averted movement away from the point of the needle.

The more I study that simple reaction, the less I am inclined to differentiate sharply between posture and movement. At the stage when the first movement occurs there is no cerebellar connection. "Posture" and "movement" are both terms invented by man, and have the serious disadvantages of all his expressions of emphasizing artificial distinctions.

DR. OLIVER S. STRONG: Would Dr. Hunt consider the difference between the movements of an atonic tabetic and a hypertonic Parkinsonian as illustrating his general view that there is a tonic component present during motion?

DR. HUNT: In my conception of the kinetic and static mechanisms, there are two kinds of tonus, *kinetotonus* which is related to the kinetic system and the disc mechanism of the striated muscle fiber and *statotonus* which is related to the static system and the sarcoplasm. Both varieties of tonus would participate in the atonia of tabes and the hypertonia of paralysis agitans, but in different degrees, depending upon the respective involvement of the two systems. In hypertonic paralysis agitans both systems of motility are in a state of hypertonus. The kinetic centers are released from control and there result the characteristic postural contractions. There is then the secondary fixation in terms of posture, because as soon as an extremity moves into its contractural attitude it becomes fixed in posture. It is the lengthening and shortening reactions of muscles on a large scale.

DR. H. A. RILEY: Will Dr. Hunt please describe the reflex pathway or pathways for the maintenance of muscular tone?

DR. HUNT: Muscle tone, according to my conception, is subserved both by the kinetic and static systems (*kinetotonus* and *statotonus*). In the static system, the chief central ganglion is the cerebellum, which has connection with the spinal cord and the cerebral cortex; the spino-cerebellar and the cerebro-cerebellar tracts. The rubro-spinal tract is the most important of the efferent pathways in the spinal cord.

The innervation in the peripheral segment, from spinal cord to the muscles, is one of the mooted questions today. There is some evidence that the sarcoplasm receives an innervation through the sympathetic for the extremities in the higher skeletal muscles. My own belief is that many of these sympathetic fibers go out in the anterior roots, and Ranson has shown the existence of large numbers of non-medullated fibers in the ventral roots, to which however he assigned a sensory function. But certainly we should not expect anything very constant in the mode of distribution of sympathetic fibers in the peripheral system because it represents so many stages in phylogenesis we must, therefore, be prepared for great differences in the mode of distribution in peripheral static innervation. In the diaphragm, for instance, it has been experimentally shown that the phrenic nerve controls movement while the sympathetic nerve controls tonus (*statotonus*).

It would appear to be unlikely that the sympathetic cords are the sole source of static innervation in the higher functions of motility (head, arms and legs).

DR. SMITH E. JELLIFFE: In view of what Dr. Strong said last night of the series of connections that the cerebellum undoubtedly had not only with the stimuli from without but with the stimuli from within, incretory stimuli and endocrine stimuli, which he grouped in a bracket as emotional stimuli—what about the emotional stimuli situations with reference to the cerebellum? In Dr. Mills' fencer, for instance, what was the position of the stomach, what was the position of the gastro-intestinal canal, what were the positions or the postural tensions, for instance, of the viscera, and what relationships might they have to the cerebellum?

DR. HUNT: I have refrained from bringing the vegetative nervous system into our discussion, but I would say that in the larger conception of my theory the static and kinetic representations exist also at the vegetative level. The sympathetic conveys static impulses, and maintains postural tone, and is the older system phylogenetically. The kinetic system is for me the parasympathetic or, as it is termed by some, the autonomic system. Of course, the autonomic has very important nuclear representations in the medulla, and so also has the sympathetic. So that there is no question in my mind but that the cerebellum would also exercise an influence over the vegetative system, through these connections, just as it exerts an influence over the segmental nervous system.

DR. FOSTER KENNEDY: Dr. Hunt, I wonder if the matter is not a little confused by phrasing; by dividing motility into "static" and "kinetic forms?" In our conversations together I have often said that these seem to me simply two forms of the same motility which exist by reason of being opposites, just as everything exists by opposites—that is, motion and inactivity, height and depth, and so on. Would not the matter be clearer if you divided all motor activity into "motility" and "tonus;" then clearly posture appears as the result of kinetic patterns, which are the union of tonus and dynamic energy and are largely produced in a great majority of our postures, by education. Postures are conditioned reflexes of kinetic dynamic motility, rather than the result of antagonism between two "forms" of motility which only exist in words by reason of being, as it were, opposite sides of the same medal.

DR. HUNT: I have thought over very carefully the question of terms and nomenclature, and I realize that any division of motility and its underlying systems is artificial, but it is the way we present ideas and the way we progress. Nature knows nothing about this sort of thing. Nature starts off with a living organism. For a million years there is perhaps nothing except posture—which assists the organism in its conflict with the surrounding forces of gravity and atmospheric pressure.

Then movement begins, as the organism becomes more complex. The point I make is that when that little movement begins you have another neural system started on its way, and as the organism grows into higher and higher complexity there are still evidences of those two systems which are very distinct and sometimes

separated in the lower forms of life. In the higher forms they are manifested by the dissociations of accident or disease.

DR. WALTER M. KRAUS: Dr. Hunt has, I believe, said that posture followed movement like a shadow. If this is so, does not posture form an element of both motile and static states?

DR. HUNT: Certainly, it does. I indicated that in my paper, and the expression that posture follows shadow-like movement. Of course, this is only a figure of speech, by which I meant to convey the idea that in movement the posturing function of muscle was also active; just as I have said that in posture the movement or kinetic mechanism is also in action. In testing sensibility, because heat is applied to the surface we do not deny the participation of the other afferent system, although heat may be the chief stimulus at the moment of observation. In the same manner I interpret posture and motion. The predominance of one function at any given moment does not preclude the participation at the same moment and in the same extremity of the other function.

DR. LEWIS J. POLLOCK: I should like to know what Dr. Hunt thinks as to what part of the postural activities of a decerebrate animal are attributable to the cerebellum?

DR. HUNT: There again, I take it that the final posture is simply the adjustment to the contractile mechanism which has been released by the decerebration. You bring about a decerebration and you release the kinetic centers. They immediately flow into their archaic manifestations of release.

DR. POLLOCK: May I ask another question to clarify this in my own mind? If, for example, we have certain demonstrable postures produced by certain definite passive movements, as turning the vertex of the head down or to the right and left, or the placing of the body against some resistance producing a movement resulting in posture, and these same postures result when the cerebellum is removed, what part of these postural activities, do you consider the cerebellum to control, and is there any demonstrable posture which can be obtained in a decerebrate preparation with the cerebellum intact which cannot be obtained in one in which the cerebellum has been removed?

DR. HUNT: There are many postural activities of a more or less reflex nature which are under the control of centers in the spinal cord and brain stem, and which function after removal of the cerebellum, just as there are many reflex movements which function after removal of the cerebral hemispheres. On the other hand, there are many evidences of a loss of postural synergy following lesions of the cerebellum. These are postural accompaniments of higher motor activities, such as are under the control of the striatum (paleokinesis) and the Rolandic area (neokinesis). And the loss of these postural synergies is what characterizes the symptomatology of cerebellar disorder.

DR. STANLEY COBB: You have obviously explained this subject extremely well from one standpoint; but perhaps we might start from another, and explain tonus on an absolutely simple reflex basis. I would like to ask if you have discarded Sherrington's idea that tonus may be explained on the basis of stretch reflexes of muscle?

DR. HUNT: The "stretch" would simply yield the afferent static impulses to the efferent mechanism. The stretch reflexes would be comparable to the lengthening and shortening reactions. Is that what you mean?

DR. COBB: No, I mean the *myotatic* reflexes described by Sherrington. In their simplest form they are more like knee-jerks. When more highly integrated these stretch reflexes combine to give postural reactions at various levels; the higher the more complex.

DR. HUNT: Of course, here you are dealing with afferent stimuli, and according to my view, two groups of afferent stimuli. There is evidence already of the existence of *statesthetic* and *kinesthetic* systems, which represent the afferent counterparts of the Static and Kinetic components in the efferent sphere.

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CHAPTER XI

THE PHYSIOLOGY OF THE CEREBELLUM¹

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DEVELOPED as it is from the region of termination of the vestibular nerves the cerebellum constitutes a group of reflex centers for the correlation and elaboration of proprioceptive impulses from the labyrinths and body muscles; aroused in this way it discharges influences which augment or inhibit the postural tone of the muscles of the body. The experimental methods used in the solution of cerebellar problems are of two kinds, namely, extirpation and stimulation. Extirpations have been performed in various classes of animals, the cerebellum being removed in whole or in part; while the purpose of complete removal was to throw light on the nature of cerebellar function in general, the purpose of limited excisions was usually to secure evidence in support of one or other of the theories of localization.

EXTIRPATION OF THE CEREBELLUM

The symptoms of cerebellar removal in the fish and amphibian are insignificant as compared with those in birds and mammals; when disturbances were observed it is not clear whether they were due simply to cerebellar deficiency or to damage to adjacent centers. Coming to reptiles we note that Leblanc observed in the lizard phenomena of cerebellar removal similar to those met with in the mammal. The decerebellate pigeon is at first unable to fly or perch; later these powers are regained, though considerable ataxia persists (1).

It is unnecessary to review in detail Luciani's classical observations on decerebellate dogs (2) and we shall confine ourselves to a discussion of some of his conclusions viewed in the light of more recent investiga-

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With the kind consent of Dr. D. R. Hooker I have used some of the material in my recent review of the cerebellum in *Physiological Reviews* in the preparation of the present paper; the material has, however, been completely revised and the results of recent work have been incorporated.

tions. With the respect to the "dynamic phenomena" of his first stage it must be stated that they owe their causation to the removal of various cerebellar regions which have an inhibitory influence on muscle tone; the symptoms may, therefore, be regarded in the light of "release phenomena."

Of the three elementary properties in Luciani's second stage, namely, asthenia, atonia and astasia, atonia or rather hypotonia has received the most attention; it is indeed regarded by several workers as the primary component in the phenomena of cerebellar deficiency (3). We must, however, now depart from Luciani so as to make reference to newer investigations, the results of which differ from his in important particulars.

Dusser de Barenne has recently made extensive studies of the symptomatology of cats and dogs deprived of the whole or half the cerebellum (4); his experiments were carefully controlled anatomically; he failed to find any evidence of hypotonia or asthenia following total cerebellar removal. On the other hand astasia or "intention tremors" formed a most noteworthy and persistent symptom, an observation in agreement with the experience of other workers. He was, further, unable to detect atonia in the limbs of the maimed side, when the head of a semi-decerebellate animal was held straight so as to exclude the influence of the "neck reflexes" of Magnus (5).

Hypotonia as a symptom of cerebellar deficiency is also rejected by Rademaker; for an account of the elaborate investigations of this writer I am indebted to the kindness of Prof. R. Magnus of Utrecht. Rademaker has developed a perfected technique for the complete extirpation of the cerebellum, using serial sections for purposes of control, until his experimental results were constant. Of a large series of dogs and cats operated on by his improved methods a number continue in excellent health two years after the removal.

Immediately after the extirpation the animals suffer from shock, in which transitory "atonia" may appear; sometimes, on the other hand, rigidity is seen at this stage, which in young animals lasts about eight days. In the succeeding period, in which the animals learn partially to compensate the disturbances of movement, one sees them creep with legs flexed, their bellies down when on hard ground; but this is not due to atonia, since on grass or straw the animals run with strongly extended legs and after a short time learn to run upright on the stone floor as well. Either standing or running they can carry

sand-bags almost as heavy as themselves. Even with powerful pressure applied to the back of the standing animal neither the fore- nor hindlegs give way. The neck and tail also show powerful tonus. In comparison with normal dogs and cats the tonus is not diminished and hence one may say that these animals do not show atonia.

It is clear, then, from these studies, the operations for which were performed under the most modern aseptic conditions, that atonia cannot be regarded as a lasting symptom of cerebellar deficiency; we note, however, that atonia or hypertonia may appear shortly after the ablation. The hypertonia is clearly due to removal of parts of the cerebellum with an inhibitory function and corresponds to Luciani's first stage of "dynamic phenomena" or more correctly "release phenomena"; here it is logical to ask if the atonia, admittedly sometimes present at this stage, does not point conversely to the removal of other parts of the cerebellum having an augmentor influence on tone and in this inference we are strengthened by the results of stimulating the cerebellar nuclei, to be mentioned later. The cerebellum can, in fact, induce positive effects, increasing postural tone, and negative effects, diminishing the same activity. Thus it appears that the reason for the failure of Rademaker to observe atonia a considerable time after cerebellar ablation is that both augmentor and inhibitory cerebellar influences are abolished; any degree of inequality between the two may well be obliterated by cerebral or other types of "compensation."

Tilney and Pike (6) have recently made an extensive study of the mode of coöperation of the antagonistic muscles in man during voluntary movements; they have also examined this relationship in the cat and monkey in the course of spontaneous movements and of cerebral cortical stimulation. They found the relationship of the two antagonists in these activities materially altered in consequence of cerebellar lesions; deep excisions of the lateral lobe yielded more marked disturbances in the ipsilateral hindleg than did superficial damage, while injury to the median cerebellar cortex caused no noticeable change in the limb. These results are thus in agreement with the view that the lateral cerebellar lobe exerts a preponderant influence over the limb muscles of the same side and that this influence exceeds that of the median cerebellar portion.

Closely related to the studies on experimental removal of the cerebellum is the investigation by Gordon Holmes of cases of cere-

bellar injury resulting from gunshot wounds (7). Owing to the inevitable delay before the patient came under examination the immediate "release phenomena" were not observed; Holmes' studies deal, therefore, with the symptoms of cerebellar deficiency, modified perhaps by various kinds of compensation.

Reviewing the symptomatology described by Holmes we note that, in agreement with most clinical observers, he always found atonia or hypotonia affecting the muscles of the limbs and, though to a less extent, those of the trunk on the side of the cerebellar lesion. It is readily revealed by flabbiness to palpation and by the greater effect of gravity in bending the wrist of the affected arm as compared with the normal wrist. In the leg it is shown by the pendular character of the knee-jerk, though the incidence of hypotonia is less severe in the leg than in the arm. These statements as to the presence of atonia are obviously opposed to those of de Barenne and Rademaker, who, as noted above, reject it as a lasting symptom of cerebellar removal. We may explain it by reference to the theory of cerebellar action already proposed in this paper, namely that some parts of the organ have an augmentor, others an inhibitory, action on postural tone: thus in Holmes' cases there would be, in consequence of the lesion, damage to augmentor centers with perhaps as well irritation of inhibitory centers.

Among other symptoms observed by Holmes the following may be mentioned:

Asthenia or weakness of the muscles of the injured side is illustrated by the lessened force shown by the dynamometer as well as by the observations of the patients themselves on the weakness and uselessness of the affected limb.

Astasia, though not an invariable symptom, is shown in the muscular tremors, the contractions being of a discontinuous, clonic nature, consequent on the imperfect sustaining of the contraction process.

Asynergia, depending on lack of coöperation among associated groups of muscles, is common: for example, a patient while standing, on throwing his head back, often falls, as a result of not flexing his knees, whereby his balance would be preserved.

Babinski's symptom, *adiadochokinesis*, the inability rapidly to perform alternate movements, is frequently encountered: thus pronation and supination are performed in a disordered way by the affected arm.

Nystagmus is always found and appears to be due to disordered postural tone in the eye muscles. Valuable corroboration is afforded for Luciani's assertion that cutaneous sensations and the sense of position are preserved intact after cerebellar lesions.

CEREBELLAR LOCALIZATION

Current conceptions on cerebellar localization are founded mainly on the hypotheses of Bolk (8), which were evolved from considerations of comparative anatomy; although Bolk's theory has found support on the experimental side from the studies of Rynberk (9) and on the clinical side from those of Bárány (10) close scrutiny of the conclusions of these writers reveals material differences from the views of Bolk. The elaborate clinico-pathological studies of Mills and Weisenburg (11) caused them to conclude in favor of some degree of localization in the cerebellum. According to these writers the functions of the cerebellum cannot be explained satisfactorily on the basis of Luciani's theory; in their opinion a more elementary property is *synergia*, by which they designate the power to associate together complex movements in the performance of definite acts. They give tentative maps of cerebellar localization but point out that the centers are not so clearly defined as in the cerebral cortex and that a particular area cannot be considered to be concerned exclusively with movements of special parts.

In spite of various divergences the observations on localization show agreement in regard to the symptoms induced in the neck and foreleg by lesions of the lobulus simplex and crus I respectively. Doubtless the control of each cerebellar half is predominantly over the same side of the body; furthermore, in the lobulus ansiformis (lateral hemisphere) there is a "prevalence of representation" of the arm anteriorly and of the leg posteriorly, though the centers for both extremities are intermingled.

Reference must now be made to one of the most remarkable discoveries ever made in the realm of cerebellar physiology. Magnus and De Kleijn and their associates in the University of Utrecht (5) have made, in recent years, extensive studies on the reflexes of posture, by which the various attitudes of the body are assumed in response to the changing needs of the organism. These reflexes include the "tonic labyrinthine reflexes," evoked through the agency of the otolith acting on the macula of the utricle; the "tonic neck

reflexes" elicited from the proprioceptors of the neck; and the various "labyrinthine righting reflexes" evoked from the saccule. All these reflexes have as their motor expression alterations in the postural tone of various body muscles. They are indeed just the kind of responses that we would naturally be inclined to attribute to cerebellar action. Nevertheless, Magnus and his collaborators found that all these reflexes persist after the complete removal of the cerebellum.

While then the cerebellum is not essential to these reflexes we must still attribute to it an important rôle in relation to muscular tone. The evidence here is largely derived from the changes in tone produced from stimulation of the cerebellar nuclei and cortex, changes which may be of the nature of augmentation or inhibition. We must be influenced further by the large number of proprioceptive fibers arriving at the cerebellum from the labyrinths and the body generally, particularly the muscles. Luciani, it will be remembered, combined Ewald's views on labyrinthine tone (12) with his own theory of cerebellar action and, considering the extensiveness of the vestibulo-cerebellar connections, there is much support for his conception. It is true that Sherrington (13) and others (5) have found the cerebellum unnecessary in maintaining the extreme tonus of decerebrate rigidity but with normal postural tone it is another matter and here we must conceive the cerebellum as supplying elements of delicate modification and control to the tonic activities of the lower centers.

ELECTRICAL STIMULATION OF THE CEREBELLUM

The excitability of the cerebellar cortex has been denied by several authors, notably by Horsley and Clarke (14), who ascribed the effects occasionally yielded by cortical stimulation to current diffusion to the cerebellar nuclei. On the other hand Mills and Weisenburg (11) asserted definitely that the cortex is excitable, since they succeeded in stimulating it in man.

The question was examined in the decerebrate cat by Banting and myself (15); we employed as a test a reaction already described by Sherrington (13), namely, the inhibition of decerebrate tonus elicitable by faradization of the front of the cerebellar cortex. Ablation of the cerebral hemispheres was performed with Sherrington's decerebrator (16), a preparation being thus obtained in which the rostral cerebellar cortex was readily available for stimulation. Bipolar stimulation was used in order that the current might, as far as possible, be confined to

the cortex. The evidence in support of the conclusion that the cortex is excitable may be shortly summarized. In the first place the reaction (inhibition of tonus) can be elicited with a very weak current, weaker in fact than is necessary to excite the cerebral motor cortex, the excitability of which is generally recognized. Secondly, it is essential for the success of the response that the cerebellar cortex be in a healthy, vascular state, the development of anaemia immediately abolishing the effect; herein lies a close parallelism with the cerebral cortex. Furthermore, we found that the response could be annulled by the superficial application of cocaine, the depressing action of which must be mainly on the cortical neurones. These data lead logically to the conclusion that the inhibition of tonus is effected in consequence of a state of excitation in the cortical neurones or, in other words, that the cerebellar cortex may be excited by the faradic current.

Cobb, Bailey and Holtz (17) stimulated the anterior cerebellar cortex and the brachium conjunctivum while recording the tonus changes in the triceps muscles on both sides; from the cortex they obtained inhibition of the ipsilateral muscle with sometimes inhibition, sometimes contraction of the contralateral muscle. Stimulation of the brachium conjunctivum yielded inhibition in the ipsilateral and contraction in the contralateral muscle. Inhibition of decerebrated tonus could be elicited from the cortex or brachium conjunctivum only if the red nuclei were retained after the decerebration.

STIMULATION OF THE CEREBELLAR NUCLEI

As is well known the various areas of the cerebellar cortex are linked to the cerebellar nuclei, which are themselves connected to the centers of the midbrain and medulla oblongata; occupying a position of such importance on the course of the cerebellofugal paths, it is obvious that their mode of action, as determined by faradic stimulation, must throw much light on the nature of cerebellar function in general.

Horsley and Clarke (14) made brief reference to results obtained on stimulating the cerebellar nuclei; they found that faradic stimulation of the nucleus dentatus yielded flexion of the elbow of the same side, while galvanic stimulation of this nucleus yielded extension of the elbow, a response also obtained to faradism when the nucleus was fatigued. Stimulation of the nucleus fastigii elicited conjugate deviation of the eyes.

A brief account will now be given of the results obtained by N. B. Laughton and myself in a somewhat prolonged investigation of this subject; a preliminary note dealing with this work has already been published (18) and a complete report will appear elsewhere. Our experiments were performed on the cat anaesthetized with chloroform and ether; the nervus accessorius is divided on the side of the cerebellar stimulation so as to avoid vitiation of our results by escape of current to the nerve, a matter often ignored by earlier workers.

The carotid arteries having been ligated and pressure being made over the vertebrals, decerebration is performed in deep anaesthesia by a cut which passes dorsally just in front of the superior colliculi and ventrally in front of the infundibulum; the nuclei rubri are thus preserved intact, a condition essential for our cerebellar stimulations. The cerebellum is next exposed and horizontal slices are removed from it so as to disclose the dorsal surfaces of the cerebellar nuclei, measures being taken to arrest bleeding and to maintain the proper temperature; in excising the cerebellar tissue it is desirable to avoid removal of the rostral cortex, the ablation of which causes intense rigidity in the foreleg, a symptom which often masks the effects of nuclear stimulation (Weed (19)).

It is necessary here to call attention to the circumstance that considerable decerebrate rigidity develops as a result of the transection of the neuraxis through the plane mentioned, *i.e.*, in front of the nuclei rubri; this observation is at variance with the conclusions of Rademaker, who claims that the tonus is normal until the large-celled red nucleus is impinged upon by the section (20). This cannot be the case in our experiments and we must relate the development of rigidity to the presence of a cortical descending tract inhibitory of tonus (Weed (19)); this tract has its origin in the "frontal lobe" (King (21)). It would appear, indeed, that just as reflex arcs concerned with movements traverse the higher level of the cerebral motor cortex so also do reflex arcs subserving postural tone, itself a reflex activity, traverse the cortex of the frontal lobe.

Following the operative procedures mentioned the animal is suspended above the table so that the reactions of its limbs may be observed; under the conditions described the forelimb on the side of the cerebellar ablation customarily assumes a characteristic posture, being flexed so that the elbow forms a right angle, the paw advanced forwards; I have called this the "hand-shake position," since it

reminds one of a trained cat giving its paw. Stimulation is applied to the exposed cerebellar nuclei by the Sherrington unipolar electrode, the diffuse electrode being secured to the lower lumbar region. Experience has shown us that the reaction most characteristic for the lateral nuclei is a further flexion of the ipsilateral foreleg; this reaction having been elicited the place yielding it is marked by inserting a small bristle; the whole specimen is then fixed in formalin and photographed; finally serial sections are made through the point marked by the bristle to determine that the nucleus was, in reality, stimulated; these sections are stained by the Weigert haematoxylin method. The following is a résumé of some of our more important results.

Nucleus emboliformis

Experiment of February 26, 1925. After exposure of the right nucleus the condition of the animal was as follows: Right foreleg, in "hand-shake position," plastic, adducted, claws extended. Left foreleg, in rigid extension. Hindlegs, in moderate extensor rigidity, less intense in the right. Unipolar faradization of the right nucleus emboliformis with very weak current, secondary distance 290 to 230 mm., yielded: Right foreleg, flexed more and drawn caudally, adducted, paw palmar flexed. Left foreleg, rigidity decreased. Right hindleg, flexed. Left hindleg, unchanged. Body curved with concavity on side of stimulation. After stimulation limbs and body returned to condition before stimulation. These reactions are shown diagrammatically in table 1. Sections showed that the electrode had been applied directly to the dorsal surface of the nucleus emboliformis (fig. 114).

The effects just described were yielded by both the rostral and caudal parts of the nucleus; the rostral part was designated by Weidenreich (22) the nucleus lateralis anterior and the caudal part the nucleus lateralis posterior; the first he considered equivalent to the nucleus emboliformis and the second to the nucleus globosus. Regarded in this way it is clear that both nuclei yield closely similar responses.

Thus we see that stimulation of the nucleus emboliformis or the nucleus globosus causes flexion of the ipsilateral foreleg as also of the ipsilateral hindleg together with inhibition of the extensor rigidity in the contralateral foreleg, a reaction which might have been flexion, had the limb not already been stiffly extended; also the body was

rendered concave on the side of the stimulation, clearly by an increase of tonus in the muscles of that side. The nuclear stimulation obviously yields augmentation of the tonus of a large number of muscle groups with reciprocal inhibition in their antagonists. An inhibitory process is clearly manifest in the relaxation of the extensor rigidity in the contralateral foreleg. The nucleus emboliformis can thus produce coördinated alterations in tonus or, expressing it otherwise,

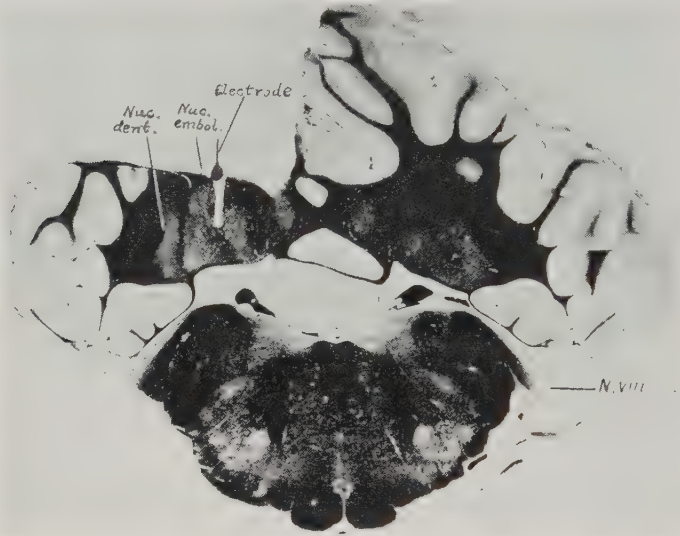


FIG. 114. Photograph of frontal section (rostral surface) of cerebellum and medulla oblongata in experiment of February 26, 1925. Weigert haematoxylin. Nuc. dent., nucleus dentatus; nuc. embol., nucleus emboliformis. Shows position of unipolar stimulating electrode over right nucleus emboliformis. Stab under electrode made by bristle marking point stimulated.

can cause changes in postural tone, both augmentor and inhibitory in nature.

A variation of the responses of the forelimbs just described is met with when both are in extensor rigidity; this condition develops in consequence of the more rostral parts of the cerebellum having been removed in making the ablation to expose the nuclei.

Experiment of October 11, 1922. Faradization over the left nucleus emboliformis yielded inhibition of the tone and some flexion of the

left foreleg with similar, though weaker, effects in the right foreleg. After stimulation there was a "rebound" increase of rigidity in both legs. In this case it is clear that flexion of the ipsilateral foreleg was impeded to some extent by the decerebrate tonus present in it; clearly both reactions are fundamentally the same. Examination of sections proved that the electrode had been applied directly to the dorsal surface of the left nucleus emboliformis (fig. 115).

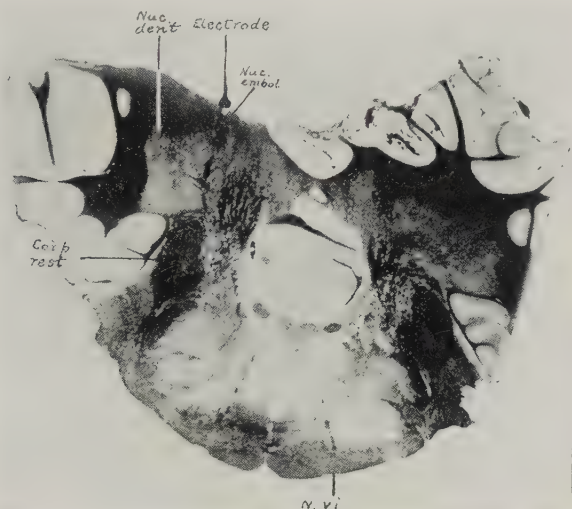


FIG. 115. Section (caudal surface) showing position of unipolar electrode over left nucleus emboliformis in experiment of October 11, 1922. Corp. rest., corpus restiforme.

Nucleus dentatus

Our observations lead us to think that the action of the dentate nucleus is somewhat similar to that of the emboliform nucleus, a circumstance dependent on the close anatomical relationship of the two nuclei. In the experiment of November 26, 1925, we found that faradization of the nucleus dentatus evoked repeated flexions of the ipsilateral foreleg with palmar flexion of the contralateral forepaw. These and other responses are shown in table X. Sections showed that a small portion had been removed from the right nucleus dentatus and that stimulation had been applied to the nucleus in that place (fig. 116).

Nucleus fastigii

In applying faradization to the nucleus fastigii it was found advisable to make a horizontal cut with the knife all the way across the cerebellum down to the dorsal surfaces of the nuclei on both sides.

Experiment of December 10, 1925. After this cerebellar ablation both forelegs were in the hand-shake position. Unipolar faradization over the right nucleus fastigii elicited strong flexion of both forelegs, the toes spread apart. After stimulation a slow extensor "rebound"



FIG. 116. Section (rostral surface) showing position of unipolar electrode over right nucleus dentatus in experiment of November 26, 1925.

took place in both forelegs. The various reactions are shown in table XI. Sections showed that the electrode had been applied just above the outer part of the right nucleus fastigii (fig. 117).

Pathways for reactions from lateral nuclei

The efferent pathways for the reactions evoked from the lateral nuclei are brachium conjunctivum, nucleus ruber and rubrospinal tract, possibly also the rubroreticular tract (23). Impulses from the

emboliform and globose nuclei pass mainly through the large-celled red nucleus and its extension, the rubrospinal tract; this is probably the route used in our most frequent reaction, that including flexion of the ipsilateral foreleg. Some of the impulses from the dentate nucleus probably follow this route, others pass through the small-celled red nucleus, rubroreticular and reticulospinal tracts. The connections of the cerebellar nuclei with the red nucleus are not as schematic as described by Marburg (24).



FIG. 117. Section (rostral surface) showing position of unipolar electrode over right nucleus fastigii in experiment of December 10, 1925. Nuc. fastig., nucleus fastigii.

Pathways for reactions from medial nuclei

The fastigiobulbar tract (fasciculus uncinatus) is probably the main pathway for the reactions evoked from the nucleus fastigii (25), reactions which have as an expressive feature flexion of both forelegs. To the explanation of the bilateral character of this response the fastigiobulbar tract lends itself admirably, since it is formed by fibers issuing from the nuclei of both sides, those from the opposite side crossing the midline (26); after looping around the brachium con-

TABLE IX

NUCLEUS EMBOLIFORMIS (RIGHT SIDE); UNIPOLAR FARADIZATION; SECONDARY
DISTANCE, 290 to 230 MM.; FEBRUARY 26, 1925

	BEFORE STIMULATION	DURING STIMULATION	AFTER STIMULATION
Forelegs	<i>Right:</i> "Hand-shake position," plastic, adducted, claws extended <i>Left:</i> Rigid extension	<i>Right:</i> Flexed more and drawn caudally, adducted, paw palmar flexed <i>Left:</i> Rigidity decreased	<i>Right:</i> Immediately returned to position before stimulation <i>Left:</i> Rigid extension
Hindlegs	Moderate extensor rigidity, less intense in <i>right</i>	<i>Right:</i> Flexed <i>Left:</i> Unchanged	<i>Right:</i> Returned to original position
Other reactions	<i>Body:</i> Straight	<i>Body:</i> Curved with concavity on <i>right</i> side	<i>Body:</i> as before stimulation

TABLE X

NUCLEUS DENTATUS (RIGHT SIDE); UNIPOLAR FARADIZATION; SECONDARY
DISTANCE, 250 MM.; NOVEMBER 26, 1925

	BEFORE STIMULATION	DURING STIMULATION	AFTER STIMULATION
Forelegs	<i>Right:</i> In partial flexion, forearm at 45° from vertical; least stimulation causes repeated flexions like progression <i>Left:</i> In moderate extension	<i>Right:</i> Repeated flexions; limb abducted <i>Left:</i> Palmar flexion of paw	As before stimulation
Hindlegs	<i>Both</i> in rigid extension, showing some progression	<i>Both</i> more rigidly extended	As before stimulation
Other reactions		Tail pointed to left. Body curved with concavity on left side	

junctivum, it passes medial to the corpus restiforme and is distributed finally to the reticular formation of the pons and medulla oblongata (27, 28).

TABLE XI

NUCLEUS FASTIGII (RIGHT SIDE); UNIPOLAR FARADIZATION; SECONDARY
DISTANCE, 200 MM.; DECEMBER 10, 1925

	BEFORE STIMULATION	DURING STIMULATION	AFTER STIMULATION
Forelegs	Both in "hand-shake position"	Both strongly flexed, toes slightly spread <i>Left:</i> Slightly ad-ducted	Slow extensor "re-bound" in both, with adduction
Hindlegs	Slight extensor rigidity with tendency to be flexed	<i>Right:</i> Flexed, toes spread apart <i>Left:</i> Unchanged	<i>Right:</i> As before stimulation

TABLE XII

EXPERIMENTAL LESIONS OF THE CEREBELLAR NUCLEI

MEDIAN GROUP		LATERAL GROUP		DEGENERATIONS				
Roof	Globus	Emboliformis	Dentate	Hook bundle	Fastigio-Deiters	Superior cerebellar arm	Red nucleus	Thalamus
Yes	?	—	—	Yes	Yes	—	—	—
Yes	Yes	Slight	—	Yes	Yes	To decus.	—	—
Yes	Yes	Slight	—	Yes	Yes	Slight	Slight	Slight
Slight	Yes	Slight	—	Slight	Slight	Slight	Slight	Slight
—	—	Yes	—	—	—	Medium	Medium	Medium
—	—	—	Yes	—	—	Medium	Medium	Medium
—	—	Yes, dorsal	Dorso-median	—	—	Strong	Strong	Strong
—	—	Yes, dorsal	Dorso-lateral	—	—	Strong	Strong	Strong
—	—	Ventral region	Ventral region	(Associations not yet determined)				

Reactions of cerebellar nuclei regarded as coördinated changes in postural tone

The reactions which we have obtained from the cerebellar nuclei are changes in postural tone both augmentor and inhibitory in nature;

they are clearly of a coördinated character involving reciprocal innervation of antagonistic muscle groups. Taken with the inhibitory capacity on tone possessed by the rostral cerebellar cortex, the nuclear responses constitute the evidence for the view already proposed by me that the cerebellar influence on tone is of both a positive and negative kind.

SUMMARY

We have in the cerebellum a series of intricate reflex arcs, which, in response to streams of proprioceptive impulses from the labyrinths and muscles, emit discharges which augment or inhibit postural tone in conformity with the attitudes and movements of the body. Besides these complex functions we may perhaps assume the existence of somewhat similar influences over impulses from the cerebral cortex.

DISCUSSION

The following questions submitted to Dr. Miller before the Commission, together with the answers to them, are here reported verbatim.

DR. CHARLES K. MILLS: Mr. Chairman, I would like to ask some questions which may appear elementary in this discussion. This is the third important meeting which I have attended, in which the functions of the cerebellum have been considered. The really splendid work which has been done at this meeting has seemed to me to fail only in one respect; that is, it has not enabled us to come to any exact decision with regard to the supreme function of the cerebellum.

I would like to question the reader of the paper, as to what his views are—for I really could not get from either his paper yesterday or today what these views were. Does he consider the cerebellum an organ of tone, or does he consider it one of synergy?

Personally, I do not think that the cerebellum is primarily an organ of tone. I do not mean to say by this, that in cerebellar diseases we do not have tonic phenomena, phenomena of exaggeration or of depression, but these seem to me to be secondary phenomena. The asthenic phenomena, in my judgment, are also secondary.

I do not think it possible to determine entirely the function of any great subdivision of the brain, by stimulation of its internal ganglia or nuclei. One shortcoming of this meeting, seems to me, to be that we have had no observations on the functions of the cerebellar cortex, brought out either by stimulative or by destructive experiments.

DR. FREDERICK R. MILLER: In answer to Dr. Mills' question, I must admit that we only seem to be at the beginning of solving some problems by the method of

stimulation. Certainly it has great limitations. I believe that by the use of these very weak currents and accurate localization, one can obtain some evidence. I do not think that it enables one to form a complete theory. The evidence that we have, taken with what we know about tone, seems to me to point to a regulation of tone, but in a special sense which I think might conform to the idea of synergy. The regulation of tone, by the cerebellum, if there is such, I think, is certainly along the lines of synergy; that is, it is coördinated.

The effects that we bring out are, of course, rather massive, exaggerated reactions, but I believe that they are not any more so than the effects obtained from the cerebral cortex, the corona radiata and from the internal capsule which have practically solved the problems of the cerebral motor cortex. I should think, on the whole, that the cerebellar control was a coördinated postural tonic affair which is very similar to what I understand is Dr. Mills' conception of synergy. It is largely a question of difference in the use of terms.

DR. LEWIS J. POLLOCK: I should like to ask Dr. Miller a question relative to the red nucleus. As I understand it, the section was made cephalad to the red nucleus, maintaining the integrity of the red nucleus, and that under those conditions rigidity was present. Were righting reflexes present or were they absent? If righting reflexes were present, then we have to deal with two elements. If righting reflexes and tonic labyrinthine and neck reflexes are both present, if the righting reflexes are entirely intact, then we should have an inhibition of all decerebrate rigidity. If, on the other hand, righting reflexes are partly lost, it would be conceivable that we may under certain conditions, for example, with the head in a position of vertex down, produce decerebrate rigidity in extension which later might in another position be changed into a flexor pattern. If that is so, then I should like to know to what you attribute the diminution in flexor tone upon cerebellar stimulation? Is it due to an augmentation of the righting reflex, which then produces a flexor pattern or is it due to an inhibition of the tonic labyrinthine tone producing a lessened extensor rigidity?

DR. MILLER: The animal, as I explained, was placed in a Czermak head-holder before decerebration and remained in that during the remainder of the experiment. Consequently, we could not test for righting or labyrinthine reflexes, but as I explained we did obtain decerebrate rigidity. That is unquestionable. It has also been obtained by others. We believe that the red nucleus was not impinged upon and probably was not interfered with. Rademaker does not mention the fact of this presence of tone when an extensive cut is made in front of the red nucleus. It is not apparent in the rabbit, which Rademaker used in his experiments, but it is quite apparent in the cat.

We found this tone, and we used it as a background for our observations. Then we stimulated and got either an increase or a decrease in this definitely present tone. How to explain it, we have not yet been able to determine.

As to whether the changes that we observe were really parts of righting reflexes and Magnus' and De Kleijn's reflexes, I believe they are very similar; probably more or less identical. I think you can excite coördinated changes in tone equivalent to reflexes from the cerebellum, just as you can excite coördinated movements

from the cerebrum. That is the chief contention. It may, or may not, be right, but it will probably start something from the standpoint of stimulations rather than of ablations.

DR. POLLOCK: I can readily understand that the rigidity which we find in decerebrate preparations may largely be present when the red nucleus is practically intact. In the work of Dr. Davis and myself, certainly we found animals where we could have at one time normal distribution of tone or increased tone in flexion or increased tone in extension. What I was concerned with particularly, in asking my question, was whether you attributed to the cerebellum the formation of these patterns of posture, or whether it modified the patterns which had been produced elsewhere? As Dr. Davis and I indicated yesterday, an ablation of the cerebellum would produce an augmentation of tonic labyrinthine reflexes which would then be entirely destroyed by destroying the labyrinth. In connection with that, I should like to know whether it is not entirely possible that the contralateral increase in tone is due rather to a tonic labyrinthine reflex than to the reflex pattern which is evoked directly from the cerebellum?

DR. MILLER: That question really raises the idea in my own mind that the cerebellum does touch off coordinated centers. I believe the midbrain and pre-spinal centers are quite competent to carry on coordinated tonus reflexes as well as coordinated reflexes of what we might call movements. The increase in tone on the one side, after the ablation, was due to the type of the ablation of the cerebellum. Stimulation of the front of the cerebellar cortex causes an inhibition of decerebrate rigidity; if you remove that part of the cortex you get an increase in tone. In some of our preparations we had removed this, and when we got inhibition, we were diminishing that great tone, so that true flexion was masked.

DR. RUSSEL MACROBERT: Warner and Olmsted (*Brain*, 1923) described tracts existing in the brain of cats which carry impulses inhibiting tonic muscular activity and state that decerebrate rigidity results when the influence of these tracts is removed. These tracts originate in the frontal lobes of the cerebral hemispheres, and the authors state that they agree in general with the so-called 'cortico-ponto-cerebellar' paths as described by Ranson. Does Dr. Miller accept their views on inhibition of rigidity?

DR. MILLER: So far as I can see, our results agree with them. They have never been accepted by Rademaker; in fact, he criticizes them quite sarcastically, but they seem to be correct. I don't think sufficient consideration has been taken of the circumstance that Rademaker worked largely with the rabbit. Sometimes he talks about an animal and does not specify which animal it is.

DR. BERNARD SACHS: Mr. Chairman, may I ask Dr. Miller for a statement of his reasons why he refused to use the bipolar method? It seems to me, with the unipolar method, however weak the current may be, there is bound to be a very large diffusion, whereas if you use the bipolar method in one very small electrode, it is made very much more easy to determine exactly where the current strikes.

Some years ago I performed some experiments along somewhat similar lines and I therefore would be particularly interested in knowing why he did not use this convenient bipolar method?

DR. MILLER: I was guided largely by my experience in Professor Sherrington's laboratory. I remembered that when we were localizing fibers from the salivary nuclei, I suggested using the bipolar method, but he claimed the unipolar method was better for fine localization. It seems to me that when you have the structure underneath your unipolar electrode and nothing deeper, that you can count on the effect. I quite admit that for many cases the bipolar is superior and we did use it solely in the work on the cortex, because we were trying to prove that the cortex was excitable; stimulating the front of the cerebellar cortex inhibits rigidity. That reaction was established by the bipolar method. I do not think the unipolar method would be so satisfactory in this particular case. However, I know that Sherrington places great reliance upon the method, and I suppose he has done more localization work than almost any other physiologist, and that is his conclusion. He would even stimulate a peripheral nerve by the unipolar method to elicit a reflex. If the reaction was powerful, with a very weak current, he was quite satisfied. When you have just one structure under your electrode, the current is concentrated just below it, Dr. Sachs, and when the current goes down just below to the one structure, I think that it is pretty certain that you are localizing it.

DR. OLIVER S. STRONG: Might not the contralateral effects be due secondarily to a reciprocal innervation performed by lower circuits?

DR. MILLER: I think the discussion has brought out some of these points. I believe that in these effects from the cerebellum we are touching off coördinating centers. The cerebellum influences postural tone, but it is further a participator in postural tone. Postural tone is a reflexly coördinated affair, brought about by the myotatic reflexes. The cerebellum can be regarded as touching off, but we can regard it also as participating with the thing that it touches off. I believe the fundamental coördinating centers are in the pre-spinal region rather than in the cerebellum.

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CHAPTER XII

EXPERIMENTAL INVESTIGATIONS OF THE CEREBELLUM¹

AUBREY T. MUSSEN, M.D.

AT A meeting of the Neurological Society of London, forty years ago, Dr. Hughlings Jackson took part in the discussion of a paper on "Muscular Hypertonicity in Paralysis." In the course of his remarks some notable views on cerebellar function were expressed which I believe will be of general interest to have recalled (12). "I submit that the cerebrum represents all parts of the body, and that the cerebellum also represents all parts of the body. But the two representations are in inverse order; putting it roughly and neglecting some parts, the cerebral order is arm, leg, trunk. This is admitted when we say that the brain is the organ of volition, for the order stated is the order of the parts as they are most often used voluntarily. The cerebellar order of representation is the opposite—trunk, leg, arm. This is admitted by those who say that the cerebellum is the organ of coördinating locomotor movements, for that expression only means an organ where muscles of all parts of the body are represented in complex ways. The order of getting parts into play in locomotion, from walking to swift running, is—trunk, leg, arm."

The extraordinary clearness of these conclusions which had been arrived at by clinical observation and deduction, are the more remarkable when it is remembered that they were made at a time when there was great confusion in regard to cerebellar anatomy. Though new cerebellar associations were being reported from time to time, they were as often denied, yet Dr. Jackson pursued his own line of reasoning which led him eventually to the belief that the cerebellum was the essential organ in locomotion and progression. Consequently it was necessary to have associated ocular movements represented; and to provide for all this it was indispensable that the cerebellar cortex

¹ From the Neurological Laboratory, Henry Phipps Clinic, Johns Hopkins Hospital.

The photographs of sections are taken from the experiments referred to. The diagrams are original.

should be the first chief station of representation of the afferent impulses from all parts of the body.

In referring to these remarks it is interesting to observe how our increasing knowledge of cerebellar anatomy has so abundantly supported them.

In the following experimental investigations on the afferent (and efferent) connections of the cerebellum some additional tracts will be described by which "muscles of all parts of the body may be represented in the cerebellar cortex;" and in the results of cortical stimulation of the cerebellum the "complex manner of this representation with associated ocular movements" will be indicated.

The results of this research, which also includes the red nuclei and the flocculus, will be considered under the following subdivisions.

I. The cerebellar connections of the posterior column nuclei of Goll and Burdach, and the tubercle of Rolando.

II. The cerebellar nuclei and their associations.

a. The nuclei considered from an experimental standpoint.

b. The connections of the median group,—the nuclei of the roof and the globosus.

c. The response of the posterior vermis and the median nuclear group to stimulation.

d. The anatomical relations between the posterior vermis and the median group of nuclei.

e. The connections of the lateral group—the nucleus dentatus and emboliformis.

III. The red nucleus in the cerebellar arc; with a criticism of the conclusions of Magnus and DeKlejn.

IV. The flocculus.

V. A preliminary report on the response of the cerebellar cortex to stimulation.

I. THE CEREBELLAR CONNECTIONS OF THE POSTERIOR COLUMN NUCLEI, AND THE SENSORY NUCLEUS OF ROLANDO

The nuclei of Goll and Burdach and the tubercle of Rolando act as central receiving and relaying stations for sensory impressions from the entire body. The impulses from the legs and lower trunk pass to the nucleus gracilis; the nucleus cuneatus serves the upper trunk, arms and neck; while the tubercle of Rolando is concerned with the impulses received from the head.

The course of the fibers which arise in these nuclei has been the subject of investigation for many years. Amongst the earliest to give attention to this problem was Flechsig (7), who in 1881 working by the myelinization method, claimed that all of the fibers from these nuclei entered the median lemniscus. Some of these he traced to their ending in the thalamus, others he followed through the internal capsule to the sensory cortex of the cerebrum. No mention was made of any fibers going to the cerebellum, but a few years later he considered it very probable that the cerebellum did also receive some fibers from these nuclei. This latter observation was denied by von Vejas (27) in the same year.

Then von Monakow (16) reported that some of the fibers of the posterior column nuclei were distributed to the cerebellum through the corpus restiforme, and claimed that these arose from the lateral nucleus of the funiculus cuneatus. This view was later supported by Blumenau, but in neither case was the distribution of the fibers mentioned.

Ferrier and Turner (1894) in their experiments found a degeneration in the corpus restiforme on the side of lesion only (6). And the investigations of Mott (1895) and Risien Russell (1897) had to do chiefly with the median fillet, no mention being made of any fibers going to the cerebellum.

The following year (1898) Tschermak (25) made lesions in the nuclei of the dorsal funiculi and described four systems of fibers: (1) A crossed system forming the median fillet which proceeded to the thalamus. (2) A crossed system which runs partly in the median fillet to the thalamus, and partly to the sensory cortex. (3) A crossed system of external arcuate fibers through the corpus restiforme to the cerebellum. (4) An uncrossed system through the corpus restiforme to the cerebellum.

In 1902 Probst (18) destroyed the posterior column nuclei on one side in dogs and cats and traced the degenerations through the corpus restiforme on the same side to the cortex of the superior vermis. He also described fibers to the nucleus of Deiters on the same side.

Then Lewnadowsky in 1904 (13) and Horsley in 1906 (10) denied that the cerebellum received any fibers from the nuclei of the posterior columns. And their conclusions would seem to have been in agreement with the generally accepted view of that time, that all afferent impressions were conveyed to the thalamus. But in the same year van

Gehuchten's researches (8) added some support to Tschermak's claim that the cerebellum did receive fibers from the posterior column nuclei; though he qualified this by stating that it was only through the dorsal external arcuates.

Since then the view that the dorsal nuclei do send fibers both direct and crossed to the cerebellum has been generally accepted, and has the approval of the more recent authorities—Winkler (28), Ranson (19) Tilney and Riley (24).

But if these conclusions are to be taken as final then the relationship between the posterior column nuclei and the cerebellum would be far from satisfactory, for the termination of all of these fibers is considered to be the anterior vermis. In fact the only connections so far described between the spinal cord and the posterior vermis are the few fibers of the dorsal spino-cerebellar tract mentioned by Ingvar (11) and Beck (2). It is unbelievable that this large posterior region of the vermis, containing folia which are in relation to the movements of the head and eyes, and certain correlated activities in the body musculature, should not be more closely associated with the nuclei of the dorsal columns of the spinal cord.

Believing that other connections from the posterior column nuclei probably existed it was decided to reopen this question, in the hope that with a greatly improved Marchi technique some interesting and possibly conclusive results might be found.

In the cat the nuclei of Goll and Burdach are represented by two elongated groups of cells approximately 8 mm. in length and 2 to 3 mm. in breadth where they extend slightly above the level of the obex. An attempt was made by means of a fine thermo-cautery to destroy these nuclei—in some cases throughout their entire extent, in others the caudal or oral portions—in order that as great a mass of degeneration as possible would result. For in some of the earlier experiments, made by transverse section through the nuclei, a comparatively small number of fibers were destroyed, which resulted in so fine a degeneration that it was difficult to follow; and though an attempt was made to limit the destruction to one or other of the nuclei, the sections always showed, as previous investigators have remarked, that the neighboring nuclei were also partially damaged.

In one of these experiments in which the degenerated area involved the nuclei of Goll, Burdach, and the tubercle of Rolando, several definite groups of fibers were found. Besides the well known dorsal

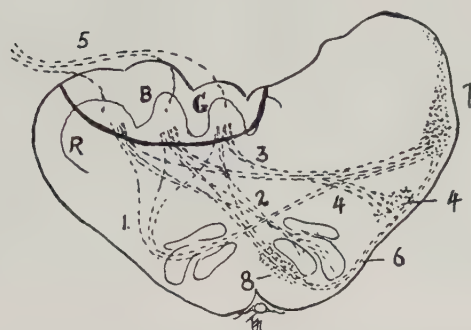


FIG. 118. Diagram of a transverse section through the medulla oblongata at the level of the posterior column nuclei. The heavy line marks the extent of the lesion which involved the nuclei of Goll (*G*), Burdach (*B*), and the median half of the tubercle of Rolando (*R*). The following degenerated fiber groups are shown: 1, direct arcuato-olivo-cerebellar; 2, crossed arcuato-olivo-cerebellar; 3, transverse arcuato-restiform; 4, transverse arcuato-extra-restiform; 5, dorsal arcuato-restiform; 6, ventral arcuato-restiform; 7, restiform body; 8, median fillet.

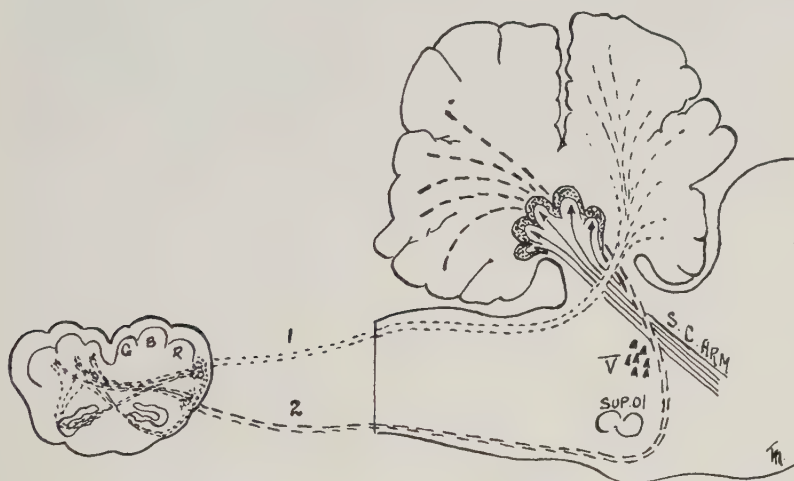


FIG. 119. Diagram illustrating the course and distribution of the arcuato-cerebellar fibers:

1. The arcuato-restiform fibers maintain a dorsal position on the oblongata, and passing lateral to the superior cerebellar arm are distributed to the anterior vermis.

2. The arcuato-extra-restiform fibers follow the ventral course taken by Gowers' tract; at the level of the superior olive they turn dorsally and passing anterior to the motor fifth, and lateral to the superior cerebellar arm they enter the cerebellum to be distributed to the posterior vermis.

and ventral arcuates which run to the restiform bodies and the fillet, five other fiber groups are to be observed.

(1) The direct arcuato-olivo-cerebellar fibers which enter the lateral region of the inferior olive of the same side, to pass out by the hilus, probably giving off collaterals *en route*. Then taking a dorso-lateral direction they enter the opposite restiform body.

(2) The crossed arcuato-olivo-cerebellar fibers which enter the opposite inferior olive through the hilus to be distributed to the cells of this nucleus.

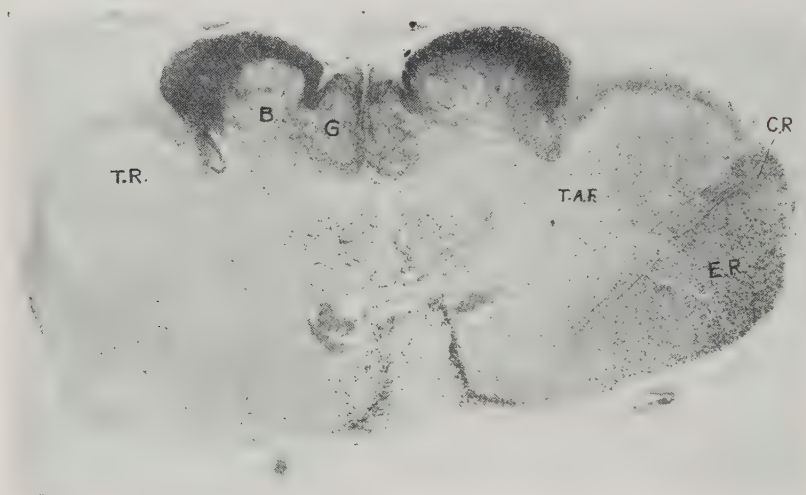


FIG. 120. The oblongata above the lesion. Degenerations in and around the nuclei of Goll and Burdach, principally on the left side. A number of transverse arcuate fibers (*T. A. F.*) passing to restiform body (*C. R.*) and to the ventro-lateral region, to form the extra-restiform bundle to the cerebellum (*E. R.*). No definite grouping of the fibers in Gower's or Flechsig's tract is found.

(3) Transverse arcuato-restiform fibers which cross the median line directly to enter the restiform body.

(4) Transverse arcuato-extra-restiform fibers which cross directly to form a compact bundle in the ventrolateral region of the medulla.

(5) Mesial fillet collaterals to the cerebellum by way of the superior cerebellar arm.

We thus have possibly five connections from the dorsal sensory nuclei and the tubercle of Rolando that have not been previously

described. The fibers which pass through the inferior olives will be considered in a later communication. At present the two tracts which cross the oblongata transversely, and the collaterals from the mesial fillet, will be dealt with as they probably play an important rôle in relation to the cortical reactions of the vermis.

Owing to the diffuse character of the lesions it is only possibly to surmise that these two groups of transverse fibers arise from the cells of the nuclei of Goll, Burdach, the nucleus of v. Monakow, and possibly in part from the tubercle of Rolando. They cross the median

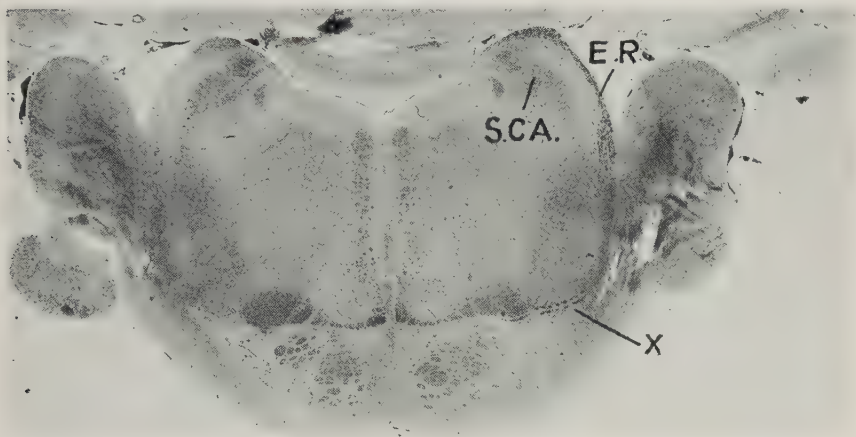


FIG. 121. Extra-restiform fibers (*E. R.*) passing dorsally to enter the cerebellum over the superior cerebellar arm. From the degenerated median lemniscus on the right side a few fibers are seen to pass laterally to join the previously mentioned group.

line transversely and then divide into a dorsal portion, the transverse arcuato-restiform fibers—which enter the restiform body; and a ventral portion—which from its course has been called the transverse arcuato-extra-restiform tract (1-5), which occupies the same ventro-lateral region of the oblongata in which the fibers of Growers' tract are found. And like Growers' tract these fibers run along the ventro-lateral surface of the stem of the hind brain to the level of the superior olive. Here they turn dorsally and after hooking over the root of the fifth nerve proceed to the superior cerebellar arm over which they swing medially to enter the cerebellum some distance from the inner

side of the fibers of the restiform body. Some of the fibers are then distributed to the roof nuclei on both sides, the remainder passing posteriorly to terminate in the pyramis lobule of the vermis. The fact that these two sets of fibers are so clearly separated and take such different paths, for they cross almost at right angles on the lateral surface of the superior cerebellar peduncle makes it easily possible to follow them to their terminations. As will be seen later these

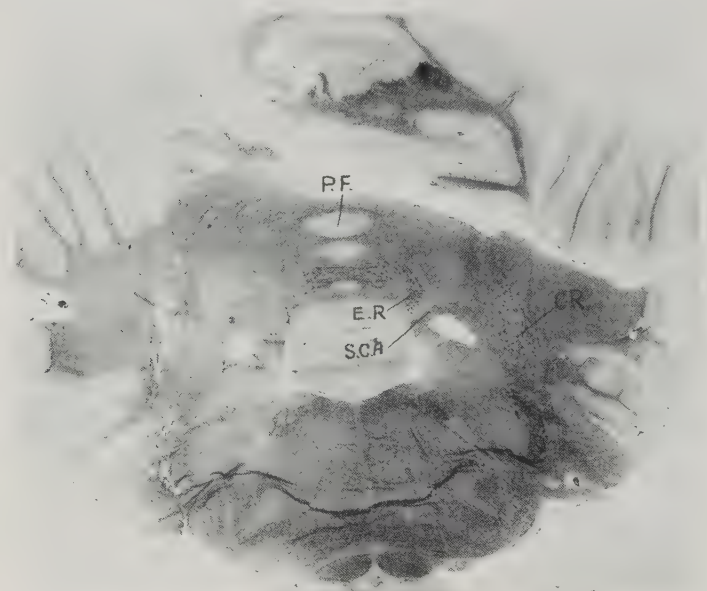


FIG. 122. The extra-restiform fibers leaving the median surface of superior cerebellar arm to the roof nuclei—posterior to the primary fissure (*P. F.*). The restiform fibers are shown laterally as they pass forward to the anterior vermis.

fibers form an important link between the contra-lateral spinal cord and the cerebellum, and will help us better to understand the reaction of the head and eyes when the posterior vermis is stimulated.

The transverse arcuato-restiform fibers (*I*, fig. 119), having united with the other groups of degeneration pass through the inferior cerebellar arm to be distributed to the anterior vermis. Thus the afferent impressions from the posterior column nuclei and the tubercle of Rolando are conveyed to both the anterior and posterior lobes of

the vermis, and there is clear evidence to support the view that these fibers are distributed to both sides.

In the same series in which the above fibers have been described, another and much smaller group has been observed. These are collaterals which are given off from the median lemniscus at the level of the superior olives. After reaching the lateral surface of the oblongata they swing dorsally to join the previously mentioned group of extra-restiform fibers to the cerebellum. These collaterals are found in every series in which the median lemniscus shows a well-marked degeneration. And it appears to be generally the coarser fibers which pass by the superior cerebellar arm to the posterior vermis, the finer fibers continuing to the thalamus. This would be in agreement with Blumenau's observation by the Golgi method that it is the axis cylinders from the large cells (of the nucleus cuneatus) that run to the cerebellum (fig. 121).

In regard to the transverse arcuato-restiform and the extra-restiform fibers the question will naturally arise as to why they have been considered to belong to the posterior column nuclei and not to Gowers' and Flechsig's tracts which their position and course suggests. After a careful examination of the sections in which their origin, course and termination have been followed, the possibility of their belonging to either of the spino-cerebellar systems has been eliminated on the following grounds. In the first place the lesion was intended to destroy only the nuclei of Goll and Burdach, and though unfortunately the sections containing the lesion are missing, the extent of the destruction can be clearly determined by the degenerations observed in the cervical cord and in the medulla.

If the destruction had been so extensive as to involve the right ventro-lateral region, both the rubro-spinal and the crossed pyramidal tracts would have been injured and a dense degeneration in the dorso-lateral region of the cervical cord would have resulted. But here we find only a scattered degeneration in the area occupied by the crossed pyramidal tract, which very probably resulted from injury to some of the fibers in the pyramidal decussation. In addition to this, if the tracts of Gowers' and Flechsig's had been destroyed there would be a very definite grouping of their fibers above the lesion, instead of which the Marchi stained sections show only a scattered degeneration. And finally the evidence indicates that these fibers terminate in the posterior vermis, while it is generally agreed that Gowers' tract is distributed to the anterior vermis.

In experimental work when some unusual feature is observed it seems only proper that it should be reported, even though proof may be lacking. So these extra-restiform fibers from the posterior column nuclei have been presented for consideration, realizing that some doubt as to their origin exists, but with the belief that future work in this field will confirm the observations.

As to the function of the nuclei of the dorsal funiculi many conflicting reports have been made. Ferrier and Turner (6) in their researches on monkeys found that after injury of these nuclei there was restlessness, sprawling of the body on exertion, and a tendency to fall backwards. The sensation to touch, pain and localization appeared unimpaired, and the disturbance in equilibrium disappeared in a few days.

Von Bechterew's dogs tumbled about on walking and swayed on standing (4). He also reported cutaneous sensation to be unimpaired.

Tschermak's cats showed at first marked disturbance in equilibrium, which soon disappeared (25). On attempting to walk they deviated toward the side of the lesion, and often fell when using the paw of the affected side. And while the contra-lateral forepaw was almost normal, the homolateral leg sprawled about on attempting to use it. Cutaneous sensation was not disturbed.

It will be observed that in each of these investigations three important facts were mentioned. Von Bechterew's dogs tumbled on walking; the monkeys of Ferrier and Turner sprawled; and Tschermak's cats fell when using the affected paw; that is to say in all these animals there was evidently a marked disturbance in the postural sense of the leg or legs affected. The disturbance in equilibrium might have been due to interference with the cerebellar connections from the posterior column nuclei, or what is more probable to injury of the spino-cerebellar tracts. In each series the cutaneous sensation was normal.

In my investigations the characteristic symptom was a loss of the postural sense in a joint, limb or limbs. Pain and temperature always appeared to be normal and equilibrium was but slightly disturbed, probably owing to the small size of the lesion. In experiment 62 which is a very good example, the nuclei of Goll and Burdach were cauterized on the right side (in the accompanying photograph). The loss of sense of position in the right foreleg was well shown, the foot being turned under the animal quietly resting on the dorsal surface. The

shoulder was affected to a less extent. From the position of the hind legs it would appear that they were also abnormal, but any awkward position into which they might be placed would be at once corrected. This was also the case with the left foreleg. Of some importance is the fact that the loss of sense of position in this and other cases *had not recovered* at the end of three weeks.

From these experiments it has been clearly demonstrated that the function of the posterior column nuclei is to convey afferent impressions from the muscles, tendons, and joints of the entire body to the cerebellar vermis and the opposite thalamus. And when it is considered that each folium of the vermis forms part of a definite synergic unit, the whole of which appears in some instances to be composed of the group of folia comprising the particular lobe, *e.g.*, the posterior vermis and the lobus centralis, the necessity of each folium receiving these afferent impressions will be realized. For only in this manner could a balance be maintained between the agonists and the antagonists, and provision made for correlating the associated muscular reactions of the limbs with the body, without which integrative synergic activity of the cerebellum would be impossible.

II. THE CEREBELLAR NUCLEI AND THEIR CONNECTIONS

a. The nuclei considered from the experimental standpoint

At the request of the secretary of the Association for Research in Nervous and Mental Diseases in 1925, I undertook to investigate the cerebellar nuclei, and to make a report at the December meeting in 1926. A grant of \$1500 was placed at my disposal to defray expenses, and the research was carried out in the Neurological Laboratory of the Phipps Clinic, Johns Hopkins Hospital.

Probably the first to give a detailed description of the central grey masses of the cerebellum, was Stilling (22) who in 1874 described the nuclei by the terms, Dachkern: Kugelkern; Pfropf; and corpus dentatum. In a beautifully finished plate of a horizontal section through the cerebellum the relative size, position and arrangement of these nuclei are shown.

Since that time it appears to have been generally accepted that there are four distinct nuclear masses, though neither anatomically nor histologically has any clear reason been advanced in support of this belief; while against it is the obvious fact that if the nuclei are ex-

amined through a complete series, it will be observed that the two median nuclei merge together, and that the two lateral are inseparably connected. Nevertheless many theories regarding the separate connections of these nuclei have been proposed. One of the most recent being that described by Marburg (15) according to which the roof nucleus gives origin to the hook bundle which is mentioned

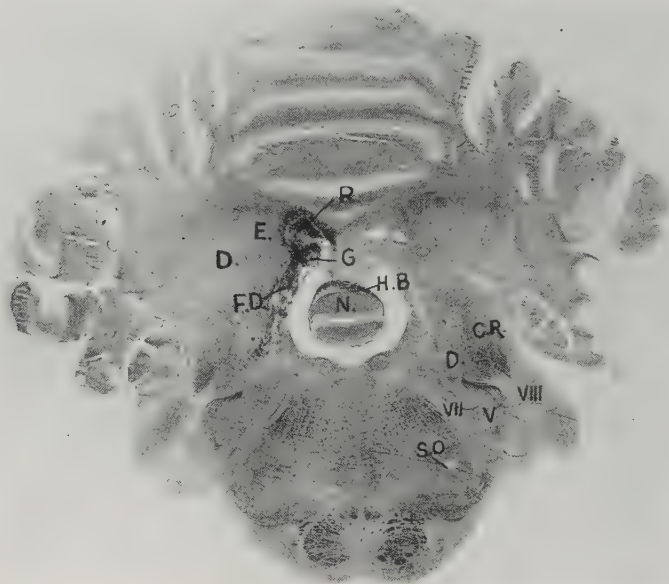


FIG. 123

FIGS. 123-126. A series illustrating a lesion in the roof nucleus and the globosus, with degeneration of the fastigio-Deiters' tract and the hook bundle. Cerebellar nuclei R, G, E, D, F, D, fastigio-Deiters' bundle. H. B., hook bundle; N., nodule; C. R., corpus restiform, D, Deiters' nucleus; S. O., superior olive; V, VII, VIII, cranial nerves. For description of hook bundle and fastigio-Deiters see text.

as terminating in the vestibular nucleus; the globosus and emboliformis are considered to send their fibers to the nucleus magno-cellularis of the red nucleus while the fibers of the nucleus dentatus run in part to the nucleus parvocellularis of the red nucleus and in part to the thalamus.

As these views are founded on human pathology and experimental results following gross lesions in animals, they are not very reliable.

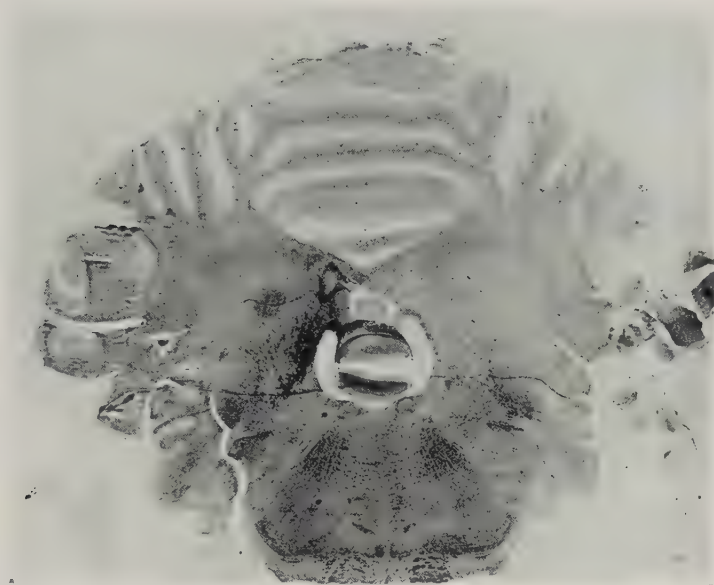


FIG. 124

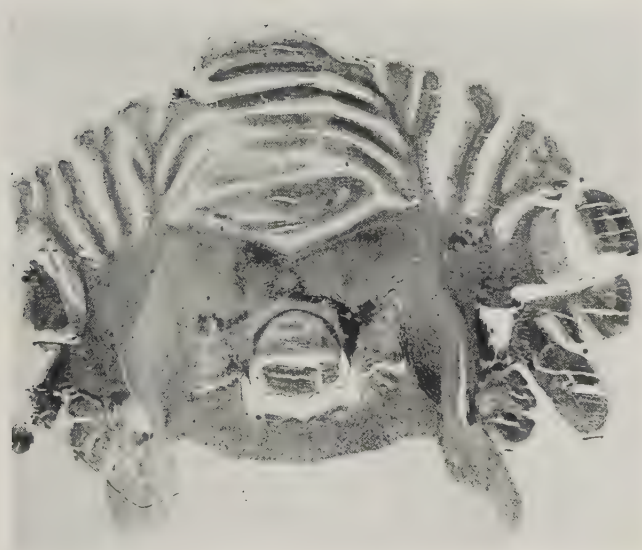


FIG. 125

How they compare with the degenerations arising from minute lesions directly in the nuclei will be considered in the discussion of the experiments.

In the following investigations the objective was to determine the relationship of these nuclei to each other, and their associations with



FIG. 126

the hind-brain, mid-brain, and thalamus. With Clarke's stereotaxic instrument a number of small lesions were made in the individual nuclei of different animals. In table XII the results have been briefly summarized.

In this table it will be noticed that when the roof nucleus alone was

injured, or the roof nucleus with the globosus, that the degenerations turned ventrally to come into relation with the nuclei of the oblongata on both sides; while if the lesion involved the dorsal half of the dentate nucleus or the emboliformis, that the degenerated fibers were only found in the superior cerebellar arm of the same side. The results therefore will be described according as the lesions involved the median group of nuclei or the lateral group.

b. The connections of the medial group of cerebellar nuclei—the nucleus of the roof and the globosus

In those experiments on both cats and monkeys in which the roof nucleus was destroyed alone or with the globosus, two distinct tracts of degeneration were observed—the hook bundle, and the fastigio-deiters, which is included in the juxta-restiform bundle. Both of these tracts connect the medial group of nuclei with the various nuclei in the oblongata. No degenerations have been found in the superior cerebellar arm.

But before proceeding with a description of these results, the work of previous investigators in this field will be briefly reviewed:

The hook bundle ("Faisceau de Crochet; Faisceau Cerebello-Bulbaire; Tractus Uncinatus; Hacken Bundle; Fibrae Cerebello-Tegmentales"). The discovery of this tract is generally accredited to Risien Russel (21) who in 1894, after an experimental ablation of one lateral lobe of the cerebellum, found a bundle of degenerated fibers occupying the hook like extremity of the dorsal region of the opposite superior cerebellar arm, an area which was quite free from degeneration on the side of the lesion. In order to prove that these fibers decussated, Russel divided the cerebellum by a median incision through the vermis and found the degenerated hook bundle occupying the same position in both superior cerebellar arms. He considered the fibers to arise from the lateral lobes of the cerebellum, and traced them to the region of the posterior corpora quadrigemina, where they became intermingled with the fibers of the opposite superior cerebellar arm.

Then Probst (18) in 1902 after removing the lateral lobe of the cerebellum with part of the vermis, and injury to the dentate nucleus, mentions among the mass of degenerated fibers, the "Hacken-bundle," but in a somewhat indefinite manner. He thought that the fibers probably arose from the roof nucleus, decussated immediately, then ran to the superior cerebellar arm on which they sat like a cap. From here they turned ventrally. But no clear description of their course or termination is given, though he suggests that some of the fibers end in Deiters' nucleus and some run to the sixth nerve nucleus.

Two years later Lewandowsky (13), following a complete hemisphere lesion of the cerebellum, reported this bundle which he called the Tractus Uncinatus. He considered that the fibers arose in the roof nucleus decussated, and then turned

ventro-laterally to hook over the superior cerebellar arm. At this point he differentiated three groups:

(1) The cerebello-tegmental fibers which run along the ventro-lateral surface of the restiform body, to terminate in the fasciculus of Roller and the fasciculus solitarius.

(2) The cerebello-vestibular portion which, after reaching the lateral surface of the restiform body, turns ventrally to descend with its medial fibers. They then turn medially through Deiters' nucleus, without ending there, and finally terminate in the nucleus of Bechterew.

(3) The fasciculus retro peduncularis, which is seen as a round bundle in the dorso-lateral region of the superior cerebellar arm. This passes oralwards and is finally lost in the grey substance of the brachium.

In 1906 Van Gehuchten (8) reported this bundle as the "*faisceau cerebello-bulbaire*," or the "*faisceau en crochet*." He credited the roof nucleus with the origin of the fibers, described their decussation in the grey mass of the cerebellum, and their course around the superior peduncle, to curve inward lower in the segment about the restiform body. He considered an anterior and a posterior fascicle; the anterior which descended into the reticular formation of the bulb, and the posterior which could be followed into the inferior peduncle. He concluded that the fibers terminated in the bulb, without knowing exactly in which grey masses their endings were to be found.

Andre Thomas (23) reviewed the literature in 1912 and performed some experiments, but contributed nothing of importance. And Marburg (15) in his *Handbuch des Neurologie des Ohres* of 1924 sums up the generally accepted view of this little known tract, by briefly stating that he considered the fibers to arise in the roof nucleus, decussate in the vermis and after hooking over the superior cerebellar arm turn ventrally to end in the vestibular nucleus.

These experiments demonstrate clearly the different opinions that existed in regard to this bundle, and how very incomplete our knowledge of its course was, with no suggestion as to its function.

When one considers the gross nature of the lesions which usually involved a quarter or half of the cerebellum, frequently with injury of the nuclei, and the very extensive degenerations that must have resulted, it is not difficult to understand that the course of any particular tract must have been almost impossible to follow.

In the present research, in which I was fortunate to have the very able assistance of Dr. Leo Bartemeier, small lesions of a few millimeters in diameter were placed directly in the roof nucleus and the globosus without injury to any other structure. From these lesions it has been possible to trace the tracts of degeneration—the hook bundle and the fastigio-Deiters' bundle—from their origin to their various terminations in the medulla; and a very definite idea as to an important part of their function has been determined.

Description of the hook bundle. Arising from the cells of the roof nucleus and the globosus the fibers of the hook bundle decussate immediately by three different routes:

(1) The main bundle leaves the ventral surface of the roof nucleus and crosses at once in the white substance of the vermis passing ventral to the opposite roof nucleus and dorsal to the lobe of the nodule, over which it swings laterally and ventrally to form a very prominent bundle on the dorso-medial surface of the superior cerebellar arm. The fibers then swing orally to hook over the superior peduncle, for it is only in sections about 2 mm. anteriorly that the bundle is found which forms a cap on the dorsal surface of the brachium. From this cap the fibers then turn ventrally, a few passing through the brachium, the majority continuing along the lateral surface of the superior cerebellar arm, then the medial surface of the corpus restiforme to the lateral region of Deiters' nucleus where they become grouped together in a very prominent bundle. The majority of the fibers then enter Deiters' nucleus where they obviously terminate.

The remainder of the fibers are then split up into three main groups.

(a) A medial bundle which sends a few fibers to Bechterew's nucleus, the dorsal nucleus of Schwalbe, and a considerable number to the sixth nerve nucleus and the posterior longitudinal fasciculus.

(b) A very compact bundle which passes ventro-laterally between the eighth nerve and the spinal root of the fifth, on the lateral surface of which it divides into two distinct branches; the lateral continuing with the fibers of the eighth nerve to an unknown destination, the nerve having been cut in removing the brain; and

(c) the median branch which swings around the spinal root of the fifth, to which it probably sends collaterals, then passes on to the seventh nucleus with which it is very possibly connected, and finally terminates in the region of the tecto-spinal tract.

A questionable degeneration was observed in the cortico-spinal tract, and around the superior olive. These relations will have to be further investigated.

(2) A second and very important group of fibers passes from the injured roof nucleus directly into the opposite roof nucleus through which it runs, most probably giving off some filaments. Most of these fibers then join the previous group, but a few continue laterally well above the superior arm and make a definite loop into the ventral region of the dentate nucleus. These fibers then pass ventrally to join the first group, none of them enter the superior cerebellar arm.

(3) A small but interesting third group turns ventrally from the injured nucleus, and swinging partly through and partly around the nodule joins the first group.

The fastigio-Deiters' bundle. This tract also takes origin in the roof nucleus and the globosus. Its course is in the mesial arm of the same side in the wall of the fourth ventricle, where it forms part of the juxta-restiform bundle, to Deiters' nucleus of the same side in which it principally terminates. Some fibers continue to Bechterew's nucleus and some pass mesially to the nucleus of the sixth and the posterior longitudinal fasciculus. In summing up the connections of the median group of cerebellar nuclei, *viz.*, the roof nucleus and the globosus—it may be said that we have:

1. The hook bundle proper, which is a crossed association with Deiters' nucleus; Bechterew's; the nucleus of Schwalbe; the fifth, sixth, and seventh nuclei; the posterior longitudinal bundle; the tecto-spinal tract; and a questionable relation with the superior olive and the cortico-spinal tract.

2. A crossed relation with the opposite roof nucleus; probably the emboliformis; and some few fibers to the nucleus dentatus.

3. The fastigio-Deiters' bundle, which is a direct association with the ipsi-lateral Deiters' nucleus; Bechterew's nucleus; the sixth nucleus, and the posterior longitudinal fasciculus.

The function of these median nuclei will be considered in the following section.

c. The response of the posterior vermis and the median group of cerebellar nuclei to stimulation

The very evident association of the roof nucleus and the globosus, through the hook bundle, with the opposite sixth nucleus the posterior longitudinal fasciculus, suggested the idea of examining the reactions of these nuclei to determine whether movements of the eyes could be obtained.

With the aid of the stereotaxic instrument a bipolar needle insulated to within 1 mm. of the points was inserted into the left side of the cortex of the posterior vermis. On stimulation a bilateral deviation of the eyes to the left occurred, with a slight accompanying movement of the head. And when the needle having passed through the cortex entered the left roof nucleus, there was a conjugate movement of the eyes to the right, with an associated turning of the head. Stimulation

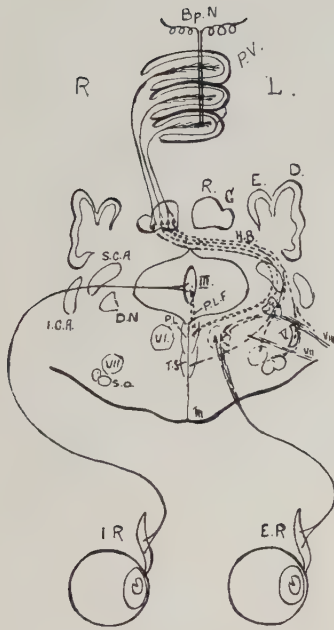


FIG. 127

FIG. 127. Diagram illustrating the conjugate deviation of the eyes to the same side on which the cortex of the posterior vermis is stimulated. *Bp. N.*, bipolar stimulating needle with 1 mm. of points exposed; *P. V.*, posterior vermis; *R.*, roof nucleus; *G.*, globulus; *E.*, emboliformis; *D.*, dentate; *S. C. A.*, superior cerebellar arm; *I. C. A.*, inferior cerebellar arm; *D. N.*, Deiters' nucleus; *III.*, third nucleus and nerve; *V.*, motor fifth; *VI.*, abducens nucleus; *VII.*, seventh nucleus and nerve; *VIII.*, eighth nerve; *P. E. E.*, posterior longitudinal fasciculus; *T. S.*, tecto-spinal tract; *I. R.*, internal rectus; *E. R.*, external rectus; *H. B.*, hook bundle.

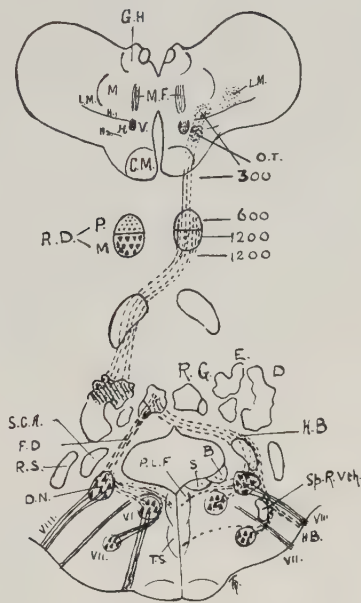


FIG. 128

FIG. 128. A diagrammatic representation of the degenerations arising from the median cerebellar nuclei—the roof and the globulus; and the lateral group the emboliformis and the dentate. *R. G. E. D.*, cerebellar nuclei; *H. B.*, the hook bundle; *S. C. A.*, superior cerebellar arm; *R. S.*, restiform body; *D. N.*, Deiters' nucleus; *VI.*, sixth nucleus and nerve; *B.*, Bechterew's nucleus; *S.*, dorsal nucleus of Schwalbe; *P. L. F.*, posterior longitudinal fasciculus; *T. S.*, tecto-spinal tract; *VIII.*, eighth nerve; *Sp. R. Vth*, spinal roof of fifth; *VII.*, seventh nerve; *R. P.*, red nucleus; *P. N.*, parvocellularis; *M.*, nucleus magnocellularis; *G. H.*, ganglion habenulae; *M. F.*, Meynert's fasciculus; *V.*, Vicq d'Azyr's bundle; *H.*, field of Forel; *C. M.*, corpus mammillare; *L. M.*, lemniscus medialis; *H. I.*, lamina ventralis and field of Forel; *O. T.*, termination of fibers in Forel's field. The numerals 1200, 600, 300 indicate the number of fibers in the different positions indicated (see text).

in the right half of the posterior vermis resulted in a conjugate deviation of the eyes to the right, and when the needle entered the right roof nucleus, the head and eyes turned to the left. These results suggested that there must be a decussation of fibers between the cortex of the posterior vermis and the nucleus of the roof and the globosus (fig. 127).

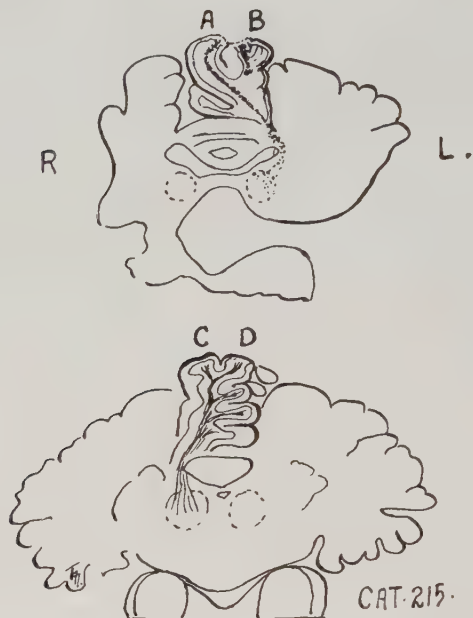


FIG. 129. Represents horizontal sections through the upper folia of the sigmoid lobe of the vermis of the cat, and demonstrates the decussation of the fibers from the cortex to the opposite roof nucleus.

A. Indicates a folium on the right side of the vermis, the fibers of which cross diagonally to reach the left roof nucleus.

B. The upper part of a folium which is continued at (*D*). The lesion involves principally the cortex at *B*, but some degeneration is also found in *A*. The degeneration starting at (*B*) is continued at (*D*) and can be followed to the right roof nucleus.

In the hope of explaining this crossed effect on stimulation, a lesion was made in one of the folia on the left side in a position similar to the one that had been excited. When the sections which had been stained by Marchi's method were examined, the degeneration was

very clearly shown to pass across the mid-line to the right roof nucleus. The explanation of this will be clear if a series of transverse sections through the posterior vermis are examined (fig. 129).

d. The anatomical relations between the posterior vermis and the median group of nuclei

In the cat the dorsal folia of the posterior vermis usually take the form of an "S" laid horizontally. The folia in the upper part of the "S" which occupy the left side of the vermis, are arranged in a triangular group with the apex pointing to the right. The folia forming the lower part of the "S" are situated in the right side of the vermis where they are grouped in a semicircle with the centre to the left. A horizontal section through the posterior vermis reveals the fact that from the folia in the upper part of the "S" that is those which lie on the left side, all the fibers pass through the apex to the right and on to the right roof nucleus; while the semicircular group of folia on the *right* side of the vermis send their fibers to the *left* roof nucleus.

What happens on stimulation then is this, when the cortex on the *left* side of the posterior vermis is excited—the head and eyes turning to the *left*—the impulse is conveyed to the *right* roof nucleus. Here it is broken up into its several components, which are necessary to bring about the combined reactions of turning the head and eyes to the left, as well as the necessary coordinated response in the general body musculature, for the main characteristic of cerebellar stimulation is a correlated muscular reaction.

The impulses which are responsible for the eye movements are then conveyed from the right roof nucleus through the decussating hook bundle to the nucleus of the left sixth and the external rectus; and by way of the posterior longitudinal fasciculus to the third nucleus and the right internal rectus, thus producing a conjugate deviation of the eyes to the left, that is the side of the vermis stimulated.

When the stimulating needle, having passed through the left side of the cortical folia, enters the left roof nucleus, we naturally obtain opposite reactions, for the impulses will now pass by the left hook bundle to the right side, to be distributed to the right external rectus and the left internal rectus, thus producing a conjugate deviation of the eyes to the right.

The accompanying movement of the head is the result of the stimulation passing from the roof nucleus to the ipsi-lateral Deiters, and by

the Deiterso-spinal tract or the posterior longitudinal fasciculus to the eleventh nucleus, thus turning the head in the direction of the eyes.

The reaction of the general body musculature will not be discussed at this time.

e. The connections of the lateral group of cerebellar nuclei—the nucleus dentatus and emboliformis

On referring to the table of experiments it will be observed that if the lesion of the roof nucleus and the globosus involves even to a slight degree the emboliformis, that a moderate amount of degeneration is found in the superior cerebellar arm, the greater part going to form the hook bundle and the fastigio-Deiters' bundle. But when the lesion involves only the emboliformis and the dentate, then the entire degeneration passes through the superior cerebellar arm of the same side to the opposite red nucleus and the thalamus. I want to mention again that in this series none of the lesions involved the ventral regions of either the dentate or the emboliformis, so that the above remarks refer to the degenerations arising from the dorsal regions only.

The superior cerebellar arm. This great efferent tract, the only direct connection between the cerebellum and the forebrain, may be described in a general way as composed of fibers which probably take their origin entirely in the nucleus emboliformis and the nucleus dentatus. Grouped together they form the superior cerebellar arm, which decussates completely, to end in the opposite red nucleus, the thalamus, and the subthalamic region.

But, as will be demonstrated, when experimental lesions involve only small areas of these nuclei, from which definite bundles of fibers pursue distinct and separate paths, then it becomes necessary to consider, not only each nucleus individually, but the particular region of the nucleus involved in the lesion. The accompanying illustrations of the degenerations arising from the nucleus emboliformis and nucleus dentatus will illustrate this.

In the nucleus emboliformis the lesion is in the dorsal region of the anterior portion. From this area the degenerated fibers form a compact bundle which occupies the dorso-median extremity of the superior cerebellar arm. The dorsal position of these fibers is maintained in the decussation. But on reaching the red nucleus where the majority of the fibers terminate, a general scattering was found both in the nucleus magnocellularis and the nucleus parvocellularis: the com-

paratively few remaining fibers then passing on to their final distribution in the thalamic region, where they occupy the Field of Forel, ventral to the lamina ventralis and lateral to the bundles of Vicq d'Azyr and Meynert.

In the dentate nucleus a lesion of the anterior region is illustrated. From this area the degenerated fibers again form a well marked tract

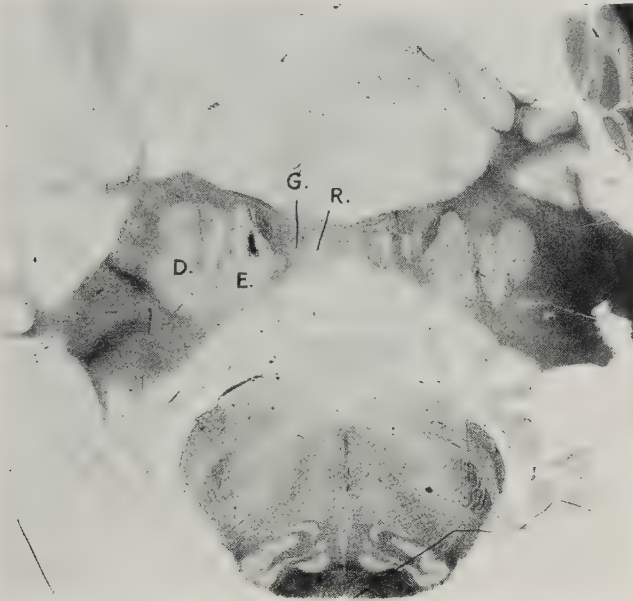


FIG. 130

FIGS. 130-132. *Macacus rhesus*. This series illustrates a lesion in the dorsal position of the nucleus emboliformis. The degenerated tract occupies a median position in the superior cerebellar arm. In the red nucleus, where the majority of fibers terminate, they are scattered. The remainder of the fibers enter the field of Forel. *R. G. E. D.*, represent the nuclei; *X*, indicates the degeneration; *F*, the field of Forel; *G. H.*, ganglion habenulae; *N.*, Meynert's bundle; *L. V.*, lamina ventralis; *V. D.*, Vicq d' Azyr's bundle.

which occupies a central position in the superior cerebellar arm. Dorso-medially, as has just been shown, lie the fibers from the oral portion of the emboliformis; the free lateral area probably serving the fibers from the ventral regions of both of these nuclei.

The central position of this bundle is maintained in the decussation; and in the red nucleus the fibers are found to be similarly grouped.

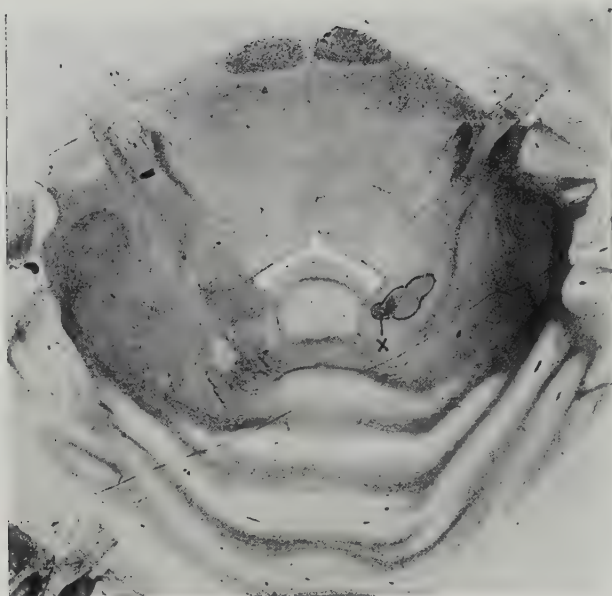


FIG. 131

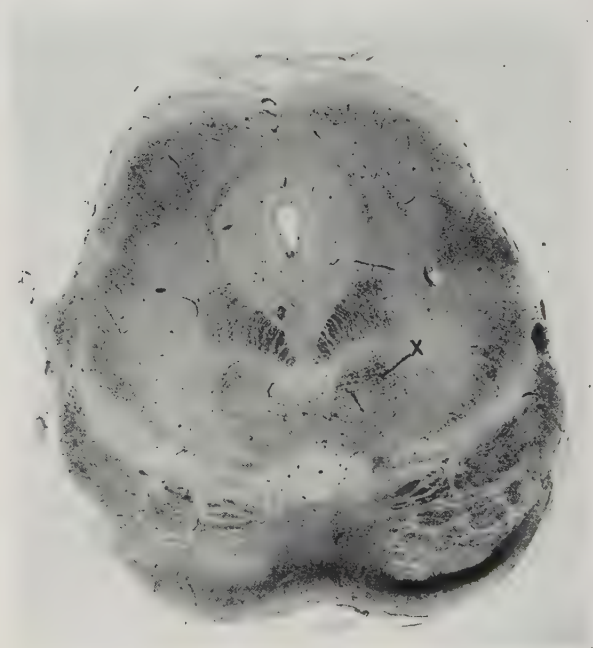


FIG. 132



FIG. 133

FIGS. 133-136. *Macacus rhesus*. Lesion of the dentate nucleus. The degeneration forms a compact bundle in the superior cerebellar arm lateral to the fibers from the emboliformis. In the red nucleus they are found grouped about the center and in the thalamus they terminate in the Field of Forel with the fibers of the emboliformis. *D.*, dentate nucleus; *E.*, emboliformis; *S. C. A.*, superior cerebellar arm; *X*, degenerated fibers; *R. D.*, red nucleus; *G. H.*, ganglion habenulae; *M.*, Meynert's bundle; *V. D.*, Vicq d' Azyr's bundle; *L. M.*, lamina ventralis.

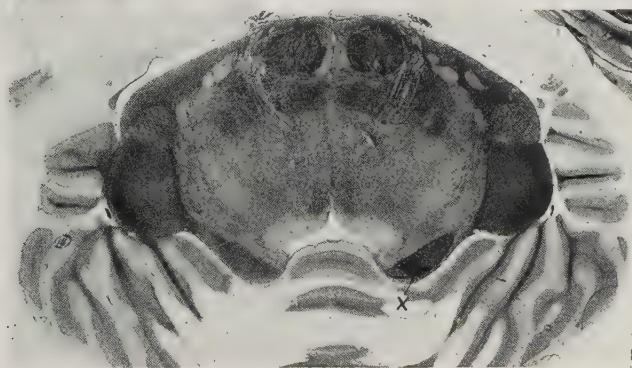


FIG. 134

But the few which proceed to the subthalamic region are found to terminate in an almost identical position as the previously mentioned fibers from the nucleus emboliformis; *viz.*, the field of Forel.

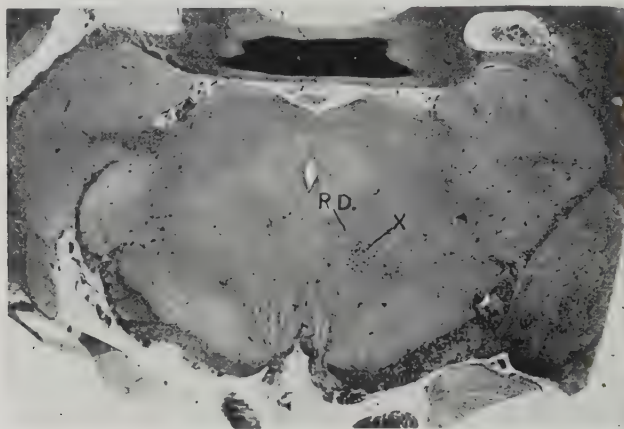


FIG. 135

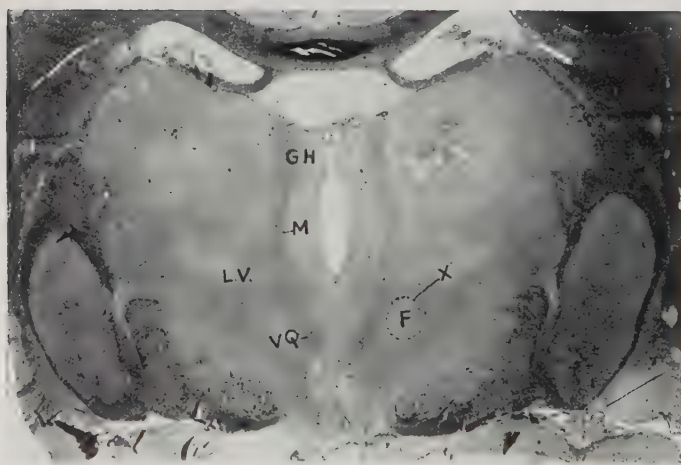


FIG. 136

In another experiment in which the lesion was more extensive, the dorsal regions of both nuclei were involved. In this instance the

terminations in the forebrain were divided. The smaller number of fibers entered the field of Forel, while the larger group occupied the postero-median region of the ventral nucleus of the thalamus, just median to the termination of the lemniscus, as observed in several unpublished experiments.

It thus appears that this nucleus of the thalamus acts as a receiving station, for the afferent impulses coming directly from the spinal cord through the median fillet, as well as for the correlated impulses from the cerebellum that reach it through the superior cerebellar arm.

In the various experiments in the emboliformis and dentate nuclei no degenerations were observed about the roof nuclei, or in the hook bundle; and the neighborhood of Deiters' nucleus was quite free.

A question of some interest regarding the degenerated fibers found in the superior cerebellar arm after lesions of the lateral nuclei, is: in what proportion do these fibers terminate in the nucleus magnocellularis, the nucleus parvocellularis and the thalamus? To determine this, the degenerations in the superior arm both before and after the decussation were counted, they totalled roughly 1200. In the nucleus magnocellularis the number of fibers was the same. The nucleus parvocellularis contained 600, while those in the thalamus numbered 300. From this it can be argued that all the fibers from the nucleus emboliformis and the nucleus dentatus enter the nucleus, any fibers that may be given off to the tegmental region being most probably collaterals. So that speaking in general terms it may be said that of a given number of fibers entering the superior cerebellar arm of the cat or monkey one-half terminate in the nucleus magnocellularis, one quarter in the nucleus parvocellularis, and one quarter in the thalamus or the field of Forel.

III. THE RED NUCLEUS IN THE CEREBELLAR ARC—WITH A CRITICISM OF THE CONCLUSIONS OF MAGNUS AND DEKLEIJN AS TO ITS FUNCTION

With the object of determining if possible the function and relations of the red nucleus, a number of experimental lesions were made on cats. During three weeks daily observations were taken. The symptoms observed will be briefly described and the results compared with those of Magnus and De Kleijn.

In the first experiment the posterior pole of one red nucleus was destroyed. No rigidity developed nor was there any disturbance in the "righting reflex."

The next step was to destroy the nucleus magnocellularis on both sides. Subsequent examination showed the destruction of the posterior poles of both red nuclei, with a complete bilateral and symmetrical degeneration of the rubro-spinal tracts. The only symptom was a slight unsteadiness in the gait which lasted two days. During the remaining eighteen days the gait was normal, and the reflexes, sense of position and muscle tone were not affected.

As such an extensive destruction of the nucleus magnocellularis on both sides, with complete degeneration of the rubro-spinal tracts, produced no symptoms, it was decided to try the effect of a lesion on the anterior pole of the red nucleus—the nucleus parvocellularis. In this experiment the lesion was limited to the anterior region of the nucleus on the left side. The nucleus magnocellularis was not disturbed, nor was there any degeneration in the rubro-spinal tract, as it is generally known. But arising from the cells of the nucleus parvocellularis a well marked tract of degeneration was observed. These fibers crossed immediately and passing under the opposite red nucleus they took up a position in the lateral region of the rubro-spinal tract field; maintaining this relation they were followed to the cervical cord in the lower segments of which they were lost. This group of fibers might be called the "*rubro-cervical tract*" to distinguish it from the *rubro-spinal* which arises from the cells of the nucleus magnocellularis and is distributed throughout the entire length of the cord.

The symptoms observed in this experiment were of great interest:

First day: The animal was found in a sitting posture, the head, body and tail curved to the right. On moving it turned in a circle to the right, pivoting on its hind legs. There was loss of sense of position in the left forepaw. Muscle tone and tendon reflexes were diminished. The "righting reflexes" were completely lost; the animal could be placed in any position—right side, left side, or on its back—and it would remain as placed without any sign of discomfort.

Second and third days: There was considerable improvement in the muscle tone and the reflexes, and the loss of the righting reflexes was not so marked in reference to the back and left side, but no attempt was made by the animal to right itself when placed on the right side.

Fourth day: There was a decided alteration in the righting reflex. When the animal was laid on the left side it got up at once. If placed

on its back it rolled over to the right and stood up. But when placed on the right side it remained lying quietly.

From the fifth day on the condition generally improved, the disturbance in the righting reflex on the right side gradually disappeared, and through the second and third weeks the only symptoms that remained were some unsteadiness in balancing, and at times a slight turning of the head to the right.

Magnus and DeKleijn (14) in their experimental work on thalamus and decerebrate animals expressed their conclusions as follows:

1. If Forel's decussation or the red nuclei are injured, then rigidity always develops and the righting reflexes are lost.

2. If Forel's decussation or the red nuclei are not injured, then muscle tone remains normal, and the righting reflexes are not affected.

In the second of my series the lesions were shown to involve the posterior regions of both red nuclei as well as Forel's decussation of the rubro-spinal tracts; that is, a condition somewhat similar to the "decerebrate animal" was produced, and there were no symptoms. According to Magnus and DeKleijn rigidity should have developed and the righting reflexes should have been lost.

In another experiment the lesion involved the anterior pole of one red nucleus, with the field of Forel anteriorly. This produced practically a "thalamus animal" which Magnus and DeKleijn state should show no disturbance in muscle tone or the righting reflexes. But in this specimen there was a marked diminution in muscle tone, and at first complete loss of the body righting reflexes which later were referred only to the side opposite to the lesion. In other words, the symptoms produced by minute lesions in intact animals were practically the opposite of those found in thalamus and decerebrate animals.

The point I desire to emphasize is that there is a great difference between the normal animals with intact central nervous systems used in my experiments, and the thalamus and decerebrate animals of Magnus and DeKleijn. In the first instance, after the minute localized lesions—about 5 mm. in extent—were made, the animals were kept for three weeks during which time the function of the central nervous system had a chance to recover (with the exception of the parts destroyed); and the structures involved in the lesion were subsequently proved by the degenerations observed in serial sections.

In the experiments of Magnus and DeKleijn we are dealing with animals which possess only the brain stem. After the operation there

is no possibility of a restitution of function, and the animals die within a few hours to a day or so. The object of course was to show by exclusion what parts were essential for the maintenance of muscle tone and the righting reflexes. But even if we allow this argument we

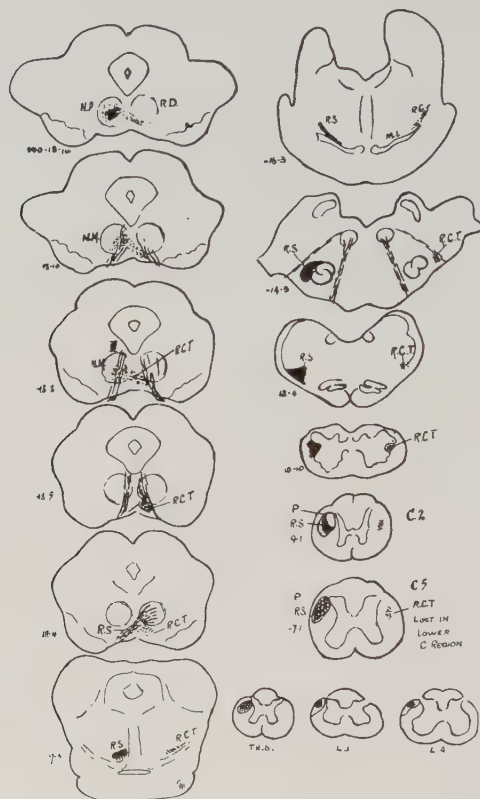


FIG. 137. Diagram showing origin and distribution of the rubro-spinal and rubro-cervical tracts, also their relative positions in regard to the crossed pyramidal tracts. *R. D.*, red nucleus; *N. P.*, nucleus parvocellularis; *N. M.*, nucleus magnocellularis; *R. C. T.*, rubro-cervical tract; *R. S.*, rubro-spinal tract; *M. L.*, median lemniscus; *P.*, outlines of pyramidal tract.

cannot overlook the fact that conclusions as to the function of a part, drawn from animals possessing only the brain stem, should be accepted with great reserve as indicating what the normal function of that part is.

The results obtained by minute lesions in intact animals which retain the possibilities of normal function through the complex association of neurones should be more reliable and more in accordance with the conditions which particularly concern both the physiologist and the neurologist, than the conclusions drawn from experiments on thalamus and decerebrate animals.

Rubro-spinal tract

So much has already been written about the rubro-spinal tract that it may seem superfluous to attempt another description. But as in no other experiment with which I am familiar have such complete degenerations been found; and as this isolated bundle can be so clearly followed throughout its entire extent in a number of experiments, one more effort to define its course and relations appears justifiable.

The rubro-spinal tract has its origin in the nucleus magnocellularis, which forms the posterior region of the red nucleus. Crossing immediately in Forel's decussation the fibers form an elongated bundle which at first lies dorso-ventrally along the median aspect of the mid-brain stem, ventral to the tecto-spinal and dorsal to the median lemniscus. In the course of its descent there is a gradual shifting laterally along the surface of the median lemniscus, till it comes to lie in the angle between the median and lateral fillets. At the level of the superior olive the fibers which are arranged in quadrangular form, are situated on its dorsal surface. Later they take the shape of an inverted comma lying around its lateral surface immediately internal to the seventh root. Opposite the inferior olive they form a triangular bundle in the ventro-lateral region of the oblongata; and at the transition of the cord into the medulla these fibers occupy the angle between the substance of Rolando and the anterior horn. In the upper cervical cord their position is within the area occupied by the fibers of the crossed pyramidal tract. In the lower cervical and thoracic segments the fibers are intermingled with those of the crossed pyramidal system; but in the lumbar and sacral regions they are again collected into a rounded bundle which occupies a central position in the crossed pyramidal area.

The rubro-cervical tract

The fibers forming this tract have been so called as they run from the red nucleus to the lower cervical cord only.

Arising from the cells of the nucleus parvocellularis some of the fibers decussate at once, passing into the opposite red nucleus possibly giving off collaterals; other fibers run posteriorly into the nucleus magnocellularis and then cross in what is probably the anterior por-

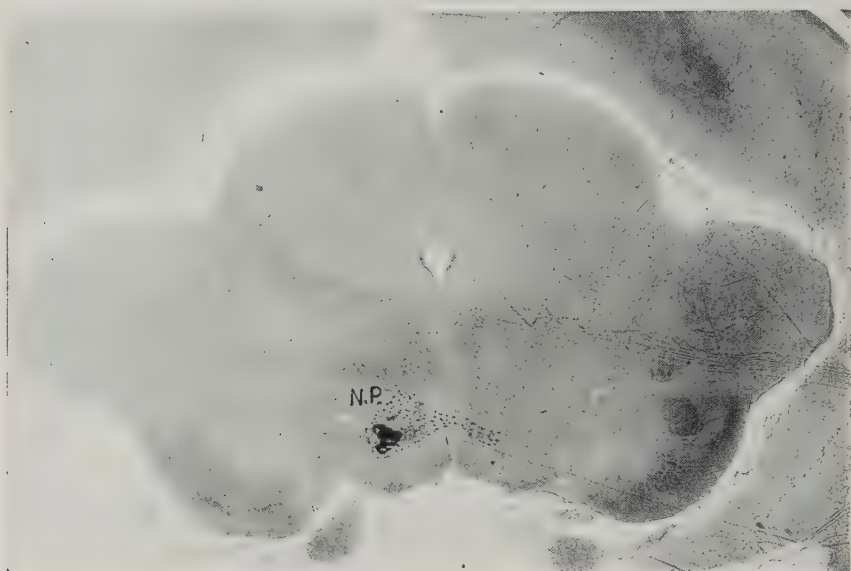


FIG. 138

FIGS. 138-143. Cat. A series demonstrating the origin, course and termination of the "rubro-cervical tract." Figure 138. Shows the lesion in the anterior region of the left red nucleus, the nucleus parvocellularis being destroyed. The degenerated fibers decussate immediately, as shown in figures 138 and 139. In figure 140 they are lying along the dorso-lateral surface of the median lemniscus. In figure 141 they form a perpendicular bundle in the lateral region of the stem. In the next section they are seen as a scattered triangular bundle in the lateral region of the medulla. In figure 142 they occupy the area between the tubercle of Rolando and the anterior horn. In the upper cervical cord they form a rounded bundle which lies within the rubro-spinal field. Figure 143 represents the lower cervical region. Here there are fewer fibers which are much more scattered. No degeneration is found in the upper thoracic segments (compare fig. 123). *R. D.*, red nucleus; *N. P.*, nucleus parvocellularis; *X*, degeneration; *R. C. T.*, rubro-cervical tract; *N. M.*, nucleus magnocellularis; *L. M.*, median lemniscus.

tion of Forel's decussation, and anterior to the decussation of the rubro-spinal tract. In a section through the posterior region of the red nucleus these fibers form a loosely arranged bundle imme-

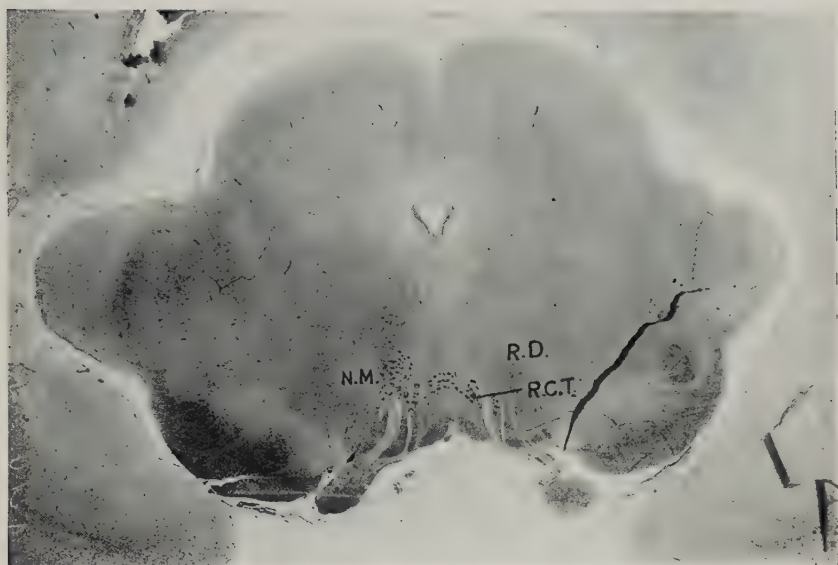


FIG. 139

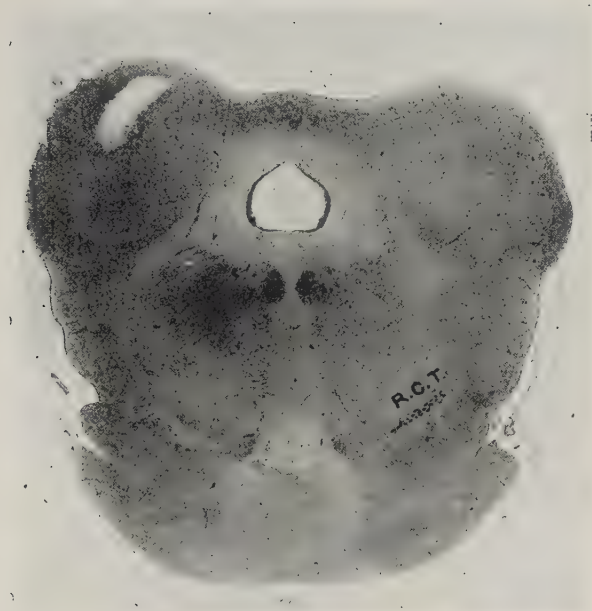


FIG. 140

diately ventral to the nucleus magnocellularis, and mostly medial to the fibers of the third root. In the brain stem the fibers are at

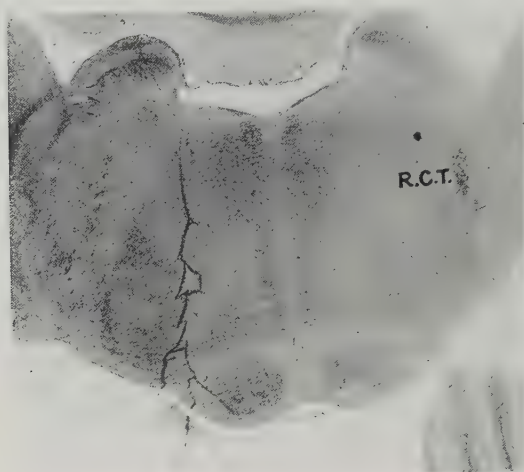


FIG. 141

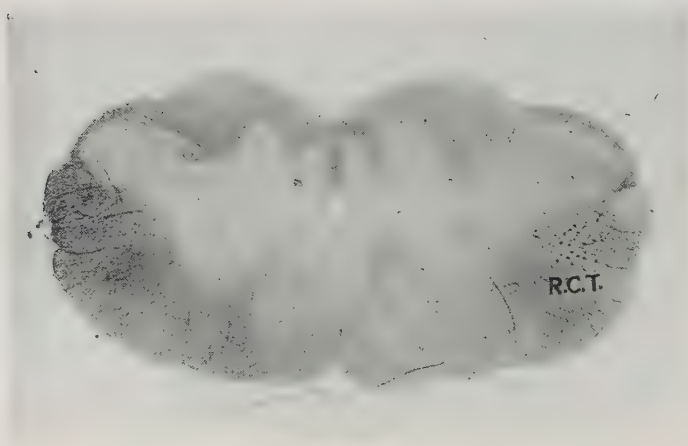


FIG. 142

first ventral to the rubro-spinal tract, then they gradually assume a lateral position when both these tracts come to lie along the dorsal surface of the median lemniscus. At the level of the superior olive

they form a small scattered bundle in the ventro-lateral region of the rubro-spinal field close to the seventh root. In the lower region of the oblongata, and through the cervical cord they are seen as diminishing group of fibers occupying the centre of the rubro-spinal tract area, and in the lower cervical region they are entirely lost (figs. 138-143).

As the rubro-spinal tract has been so frequently illustrated, the series of photographs of the unilateral and bilateral lesions of the red nucleus have been omitted. But in the accompanying sketch of a series of sections from the red nucleus to the sacral cord, the position

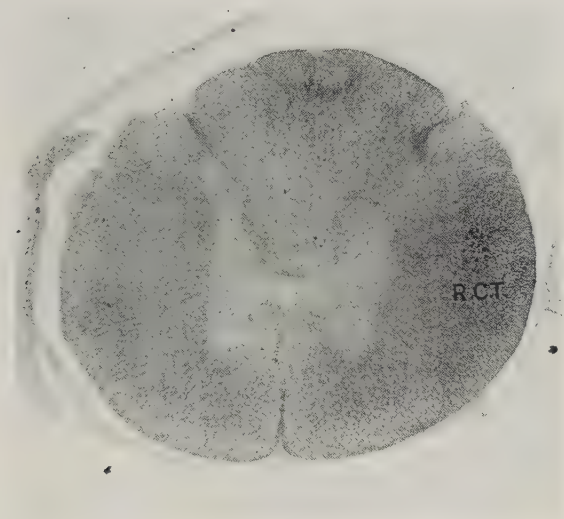


FIG. 143

of the rubro-spinal and the rubro-cervical tracts is shown for comparison, and their relation to the crossed pyramidal system is indicated (fig. 137).

IV. THE FLOCCULUS

Bárány's experiments on the flocculus (1) were principally concerned with stimulation. In a number of animals he showed very clearly that the effect of cortical excitation of this portion of the cerebellum resulted in various combinations of eye movements.

In my experiments an attempt was made to destroy the flocculus in the rabbit. Though only a portion of one flocculus was removed,

such very definite symptoms resulted, which I believe have not been previously observed, that it seems advisable to report them. On examining the animal a few hours after the operation it was noticed that the "righting reflex" on the side of the lesion was completely lost, and this state persisted with the eyes open or bandaged. A series of very interesting motion pictures show that the animal quickly rights itself when laid on the sound side; but when placed on the operated side there is no response until the animal is aroused by pinching.

As the preparations of these experiments have not yet been examined, the anatomical description of the lesions will have to be reported later.

V. SOME PRELIMINARY REMARKS CONCERNING THE RESPONSE OF THE CEREBELLAR CORTEX OF THE CAT TO STIMULATION

a. The vermis

Encouraged by the results obtained on stimulating the cortex of the sigmoid lobe already referred to, an investigation of the reactions in the other lobes of the vermis was undertaken. In these experiments the cortex alone was stimulated, in no instance did the needle enter the nuclei. The general results of these reactions is summarized in the accompanying diagram, representing a medial sagittal section of the vermis (fig. 144).

On examining these reactions it is interesting to note how muscle responses which are closely associated physiologically are grouped together to form a synergic unit.

In the ventral lobes—the uvula, nodule and lingula—we find the movements concerned in swallowing represented, *viz.*, contraction of the muscles of the throat, movements of the lips and tongue, as well as some associated head and eye movements.

The lobus centralis gives a very interesting correlation of the muscular reactions that are necessary to enable the animal to look upward—eyes turned up, elevation of upper lids and eyebrows, and contraction of the posterior neck muscles.

The culmen—is apparently concerned with the reactions of the muscles on the side of the neck—the anterior and lateral neck muscles, the temporal and ear muscles, as well as various eye movements.

The folia of the declive give reactions in the lateral neck muscles, the shoulder being raised and head bent over sideways. There are also eye movements to the side stimulated.

In the pyramis we have as previously shown conjugate movements of the eyes to the side stimulated, with some movements of the head.

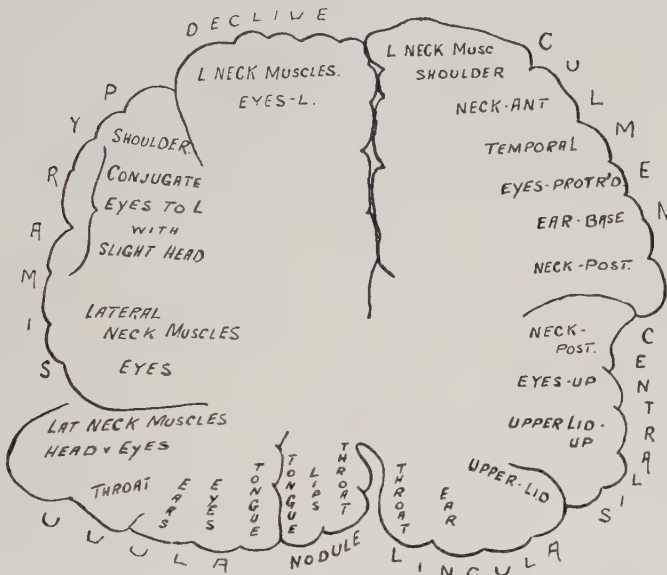


FIG. 144. Diagram of a sagittal section of the cerebellar vermis of the cat, showing the group reactions obtained on stimulation of the various lobes of the cortex.

b. The cerebellar hemisphere

If the cerebellum of the cat is presented on a plane surface the composition of the various lobes and their relations is quite obvious. In describing these the simplest nomenclature has been used; viz., the pennate, the paramedian and the vermiformis (fig. 145).

The pennate lobe, which consists of anterior, lateral, and posterior lobules, forms the bulk of the dorsal surface of the hemisphere. Stimulation of the anterior lobule results in responses of the muscles of the shoulder and chest, with some eye movements. The lateral lobule gives reactions in the shoulder and temporal muscles; while the posterior lobe is concerned with the shoulder and jaws. Various eye movements were also observed.

The paramedian lobe shows responses in the muscles of the shoulder, upper leg and fore-leg, with supination of the fore-paw, extension and protrusion of the claws, and closure of the jaw. Some associated eye movements have also been noted.

The vermiform lobe which is very difficult to get at has not been thoroughly examined. But it may be said from the reactions so

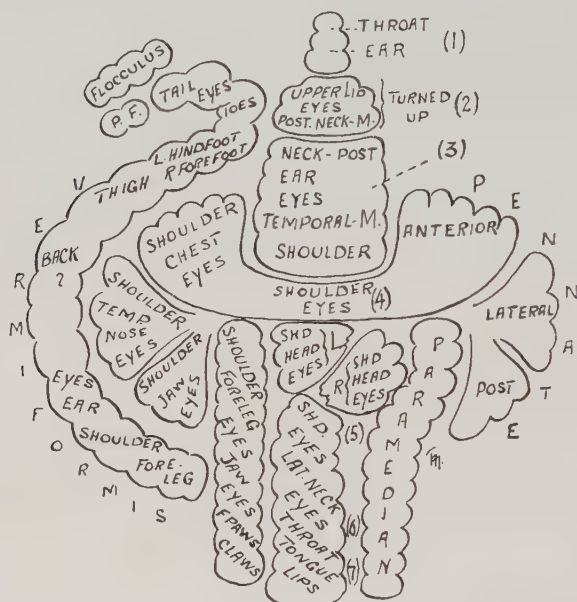


FIG. 145. The cerebellum of the cat presented on a plane surface. The lobes of the vermis are indicated by the numbers 1 to 7: lingula; centralis; culmen; declive; pyramis; uvula; nodule. The hemispheres are made up of the pennate lobe, the paramedian, and the vermiformis. The most important group responses which were obtained on stimulation of the cortex of the folia comprising these lobes is shown.

far obtained that this lobe is concerned with the movements of the trunk, limbs and tail. The posterior folia give responses in the foreleg with some eye movements. The folia of the lateral region are probably concerned with the movement of the muscles of the back. While the anterior folia give reactions in the thigh, hind leg, hind paw, toes and tail, which was moved to both the right and the left. In all these reactions there are usually some associated eye movements.

These cerebellar cortical responses which are so briefly reported, have not only been very definitely localized to the side stimulated; but if a similar position in the opposite hemisphere is excited an exactly similar response in that half of the body is obtained. There is little doubt that these reactions are in the main correct, and there is no question of these results being due to the so-called *spread* of the current.

It must though be emphasized that this is but a preliminary report on the reactions obtained in the cat. Many questions naturally arise, and much work has yet to be done. It is my intention to continue with this problem so that it may be possible to present a more detailed account at a future meeting.

These results naturally lead me to the conclusion that the cerebellar cortex is directly responsive to stimulation, and that the character of this response is a correlation of the various muscular reactions which are concerned in some physiological activity; *e.g.* the conjugate movement of the head and eyes to the right and left on stimulating the posterior vermis, the associated movements which enable the animal to look upwards as found in the lobus centralis: and the movements concerned in swallowing which are represented in the ventral lobes.

It is realized that these conclusions are opposed to those of previous investigators, and that they are based on experiments that are not yet complete, yet as the character of these reactions has throughout been so definite I feel it advisable to present these views now so that an opportunity will be offered for the consideration of this much discussed and very important question.

The following localized and correlated reactions, obtained by stimulating the different folia of the cerebellar cortex, were demonstrated by motion pictures.

1. Posterior vermis, first folium of the left lobus pyramis; movement of the right shoulder.
2. Posterior vermis, first folium of the right lobus pyramis; movement of the right shoulder.
3. Posterior vermis, second folium of the left lobus pyramis; movement of the left shoulder, head and eyes to the left, twitching of the right ear.
4. Posterior vermis, left side of uvula; movement of the left shoulder, ears and jaw; vertical movements of the eyes.
5. Nodulus of the posterior vermis; movements of the jaw, with slight throat and tongue movements.

6. Anterior vermis, left side of the lobus centralis; movements of the left side of the face, left shoulder and neck.

7. First folium of the left paramedian lobe; movement of the left shoulder.

8. First folium of the right paramedian lobe; movement of the right shoulder.

9. Second folium of the right paramedian lobe; movement of the right shoulder, extension of the right fore-leg, head to right and lateral eye movements.

10. Third folium of the right paramedian lobe; movement of the right shoulder, flexion of the right fore-leg, eyes to left and pupils dilated.

11. Fourth folium of the left paramedian lobe; movement of the left shoulder, left fore-paw and left eyebrow, rotatory movements of the eyes.

12. Anterior folium of the left lobus vermiformis; movement of the tail to the left.

In conclusion I wish to thank Dr. Adolf Meyer for his unfailing support and helpful criticism through the various investigations.

To Dr. Frederick Tilney and Dr. T. H. Weisenburg I am also deeply indebted, both for their stimulating interest in the work as well as for the grant from the Association for Research in Nervous and Mental Diseases, without which the research on the cerebellar nuclei had been impossible.

Dr. Leo Bartemeier's very able assistance during the early period of the work, and in the presentation of the "Hook Bundle" at the meeting of the American Neurological Association at Atlantic City in 1926, is gratefully acknowledged.

And I desire also to express my thanks to Miss C. Bisson for her careful supervision of the laboratory technique, the excellent photographs, and the motion pictures.

DISCUSSION

The following questions submitted to Dr. Mussen before the Commission, together with the answers to them, are here reported verbatim.

DR. FREDERICK TILNEY: I would like to ask Dr. Mussen with reference to one of the components of degeneration shown in the superior brachium and passing

the red nucleus to the thalamus, whether he has any explanation to offer as to the possible functional significance of that bundle? What I have in mind is this: You are showing in your experiments a series of fibers which pass beyond, in a certain sense, the supra-segmental cerebellar arc, passing up toward and presumably into the supra-segmental zones of the cerebellum. Do you think that it might be the case that these fibers imply somewhat the same thing that the proprioceptive fibers in the mesial fillet imply as they go up alongside of it?

DR. AUBREY T. MUSSEN: An answer to this question must be largely theoretical, as in none of these experiments were any symptoms observed; and the degenerations have not been traced beyond the thalamus.

Lesions of the lateral cerebellar nuclei—the emboliformis and the dentatus—give rise to fibers, the majority of which end in the opposite red nucleus. The remaining fibers, approximately one-quarter, pass on to the thalamus. Of these some terminate in the medial region of the ventral nucleus adjacent to the fibers of the mesial fillet which are situated laterally; and some end in the field of Forel.

This arrangement suggests that the first group of fibers may serve the purpose of conveying the results of cerebellar activity to the thalamus to supplement the proprioceptive impulses carried by the mesial fillet. The fibers which are found in the field of Forel are possibly concerned with the transmission of cerebellar impulses to the lenticular nucleus. The resulting correlation of impulses is then brought under the influence of the red nucleus, the final reaction of this striato-rubro-spinal system being concerned with automatic and associated movements.

DR. TILNEY: Have you attempted any of these stimulation experiments on the apes, where the vermis of the cerebellum is so conspicuously different? In the apes it has none of that sinuous twisting which you show, and which seems to account for the shifting of the cortex-roof nuclear connections.

DR. MUSSEN: The first stimulation experiment of the cerebellar cortex was tried on the *Macaccus rhesus*. Having observed in the degeneration of the hook bundle how the roof nucleus was connected with the opposite sixth, I was interested to see what would result if the roof nucleus was stimulated.

When the needle was inserted into the cortex of the posterior vermis on the left side, there was a very definite conjugate deviation of the head and eyes to the left—the side of the cortex stimulated. On stimulating the left roof nucleus the head and eyes turned to the opposite side. Stimulation in the right side of the posterior vermis resulted in the head and eyes turning to the right; while on stimulating the right roof nucleus the head and eyes turned to the left.

DR. WILLIAM G. SPILLER: At a recent meeting of the American Neurological Association, I reported a case most carefully studied by Dr. Isaac Jones of Los Angeles, by the Bárány tests. Eleven days before the boy died he determined that there was complete loss of all vestibular function and complete integrity of all cochlear function. The brain was sent to me by Dr. Jones and serial sections were made. Complete degeneration of the central portion of the tegmentum of the medulla oblongata was found, extending from above, where the vestibular nerves make their entrance. That lesion caused complete loss of the function of the

vestibular nerves. In looking at your specimens I noticed that some of the fibers which you represent as the hook bundle seem to come far forward in the medulla oblongata. Can it be that those fibers have a relation to the vestibular nerve?

DR. MUSSEN: There apparently is a very close association between some of the fibers of the hook bundle and the vestibular nerve, as many of them end in Deiters' nucleus. Collaterals also enter the triangular nucleus of Schwalbe, and a very distinct bundle leaves the medulla along the eighth root. The course of these fibers was not followed as the nerve was cut in removing the brain.

DR. LEWELLYS F. BARKER: I would like to ask whether the lesions permit Dr. Mussen to differentiate between the fibers from the dorsolateral part of the nucleus dentatus and those from the frontomedial part of that nucleus, and if so, whether there is any difference in the distribution of the two sets of fibers?

DR. MUSSEN: It is not possible at the present time to answer this question definitely, as many of the results have not been completely examined. But some idea may be obtained from the two following experiments.

In No. 1 a very small lesion was found in the anterior part of the nucleus dentatus. This gave rise to a compact bundle of degenerated fibers which occupied a medial position in the superior cerebellar arm; was centrally grouped in the red nucleus; and terminated in the field of Forel.

In No. 2 a much larger lesion destroyed the dorsal half of the median portion of the nucleus dentatus. This resulted in a diffuse degeneration in the superior cerebellar arm and in the red nucleus. In the thalamus some of the fibers were found in the medial region of the ventral nucleus, and some in the field of Forel.

DR. ADOLF MEYER: It might interest all of us to know if, besides the stimulation result of deviation of the eyes, Dr. Mussen has observed certain lasting defects from the various injuries of the nuclei, or whether the lesions were too small to produce any defect symptoms?

DR. MUSSEN: In regard to symptoms, the experiments on the cerebellar nuclei have not been instructive. The lesions which were intended to be small in order that definite isolated degenerations would result, produced so little damage that no clinical disturbance was observed.

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CHAPTER XIII

THE INFLUENCE OF THE CEREBELLUM UPON REFLEX ACTIVITIES¹

LEWIS J. POLLOCK, M.D., AND LOYAL DAVIS, M.D.

TILNEY and Pike (1) have proposed the conception of simultaneous contraction in the operation of synergic muscular units, and attribute to the cerebellum the important rôle of maintaining the proper relation in the synergic units of the body. "Its proper function seems to be the proportional adjustment in time and extent of the increment of muscular tension."

This work again brings to our attention the controversial subject of the functional relations of antagonistic muscles. In their work, Tilney and Pike were concerned with voluntary action and experimentally produced movement by electrical stimulation of the cerebral hemispheres, midbrain and spinal cord. Obviously, the movements resulting from such electrical stimulation differ widely from those produced by reflexes induced by peripheral stimulation. It is unnecessary to review the literature upon the functional relation of antagonistic muscles since Tilney and Pike have adequately and critically presented it. It is interesting, however, to refer to their quotation of the results of Beaunis' experiments.

His analysis seemed, therefore, to show three distinct varieties of intermuscular relation during contraction: first, the antagonists or groups of antagonists contract simultaneously. This is the normal case and according to Beaunis by all means the most frequent. Second, a single one of the two muscles may contract while the other remains motionless. This is an exception. Third, one of the muscles contracts and the antagonist lengthens and relaxes.

It is our purpose to show that insofar as tonic labyrinthine and neck reflexes and certain nociceptive reflexes are concerned, all three varieties may be obtained in the same synergic unit under certain

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conditions at will, and that the removal of the cerebellum does not affect this type of functional relation.

Much of the difference of opinion in regard to reciprocal action of antagonistic muscles is due to differences and faults of technic. Some is due to an attempt to compare one type of movement with an entirely different one. For example, that produced by cortical stimulation with that produced by peripheral stimulation or voluntary movement. Further discrepancies may be attributed to the type of stimulus and character of the reflex arc. For example, proprioceptive and tonic reflexes as compared to nociceptive reflexes.

Although, from a study of parts of certain reflexes, and movements produced by electrical stimulation of the cerebral cortex and extra-ocular muscle movements, Sherrington (2) presented convincing evidence of reciprocal innervation, he recognized that,

A change of internal conditions may presumably convert an intraspinal condition that under the primary conditions is inhibitory, into one that later under supervening conditions becomes excitatory. The fact that under certain forms of cerebral action true antagonistic muscles can be thrown synchronously into contraction points to the same limitation of the term "specific" in this condition.

Beritoff (3) has conclusively shown that at the period of intense extensor rigidity in a decerebrate animal, the tonic reflexes chiefly assume the form of increase or decrease of this "spontaneous" extensor rigidity. The amplitude of tonic contraction of the extensors increases or decreases according to the position of the head. The flexors remain all the while in complete repose; that is, both when the position of the head is optimum for the extensor tonus and when that position is reversed. At this time ipsilateral sensory nerve stimulation produces a much weaker effect than when extensor rigidity is considerably reduced. When extensor rigidity is weakened with the head in a position favorable for flexor tone (vertex up), contralateral sensory nerve stimulation produces but a feeble contraction of the extensors, but when the head is turned vertex down a strong contraction results. This reciprocal relation of antagonists does not relate particularly to the simultaneous contraction or relaxation of antagonistic muscles, but largely to the reciprocal increase or decrease of tone and stimulability in opposing muscles when the tonic labyrinthine reflexes augment their respective tone.

Beritoff (4) later studied the rôle of labyrinthine and neck reflexes

in reflex action evoked by peripheral stimulation in the decerebrate preparation. He here called attention to the observation of Graham Brown that in the ipsilateral flexion effect of the decerebrate preparation it often occurs that contraction appears in the extensor as well. This contraction Beritoff showed to be dependent upon the position of the head. The extensor contraction which occurred simultaneously with the flexor one upon ipsilateral stimulation when the head was twisted face upward, failed to appear when the head was twisted face downward. In the ipsilateral extensor reflex produced by weak stimuli, a slight flexor contraction was noted preceding and at times during the extensor contraction. The amplitude of this contraction depended upon the position of the head. This so-called "decerebrate type" of reflex must be regarded as the result of simultaneous excitation of the protective flexion reflex and of the tonic extensor reflex from the influence of the neck and labyrinthine extensor centers. In his communication in 1914 he called attention to nontonic reflexes preceding the tonic ones when the head was turned from side to side. "In some preparations, a transient contraction of both antagonistic muscles preceded the tonic reflexes and at the same time the tonic reflexes themselves appeared with distinct reciprocal relations." All this shows that rapid change in the position of the neck produces, together with purely tonic reflexes, special reflexes the character of which is not tonic.

Although he does not analyze his tracings for special evidence of cocontraction or reciprocal innervation, an examination of the tracings illustrating his articles shows that cocontraction occurs in the nontonic reflex preceding the tonic one, in the ipsilateral extensor reflex, in ipsilateral flexor reflexes with and without removal of the cerebellum, and in a contralateral extensor reflex. It is notable that in most instances after the initial cocontraction, when the extensor relaxed, the flexor showed an increment of tone and vice versa. The changes in tone consequent to turning of the head, which were tonic in nature, all showed reciprocal innervation.

Our material consisted of spinal animals, animals decerebrated by the anemic method, and by a saw, before and after removal of the cerebellum. In the anemic decerebrate animals the cerebellum was rendered functionless by cutting, coagulating or tying the posterior-inferior cerebellar arteries; the superior cerebellar arteries already being functionless as the result of the carotid and basilar artery ligatures.

The muscle preparations were made with particular care as to careful separation of muscle planes, conservation of nerves and fixation of all segments about joints by pegs driven through the bones into the

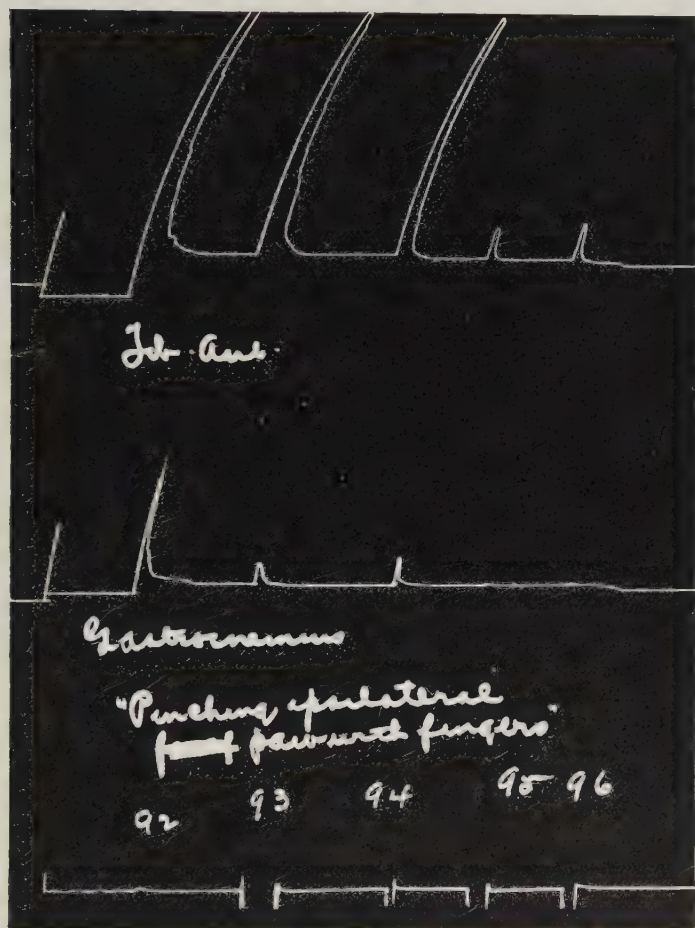


FIG. 146. Cocontraction resulting from pinching ipsilateral hind foot with finger in a spinal animal.

animal board. Linen sutures were placed into the severed tendons of antagonistic muscles and fastened directly to a muscle lever to which a counterweight was applied.

With regard to the character of the tracings, attention must be called to the difference in the technic of severing one tendon (for instance, the flexor) and observing by palpation the tone in the extensor muscle when a flexor reflex is evoked, and that of severing

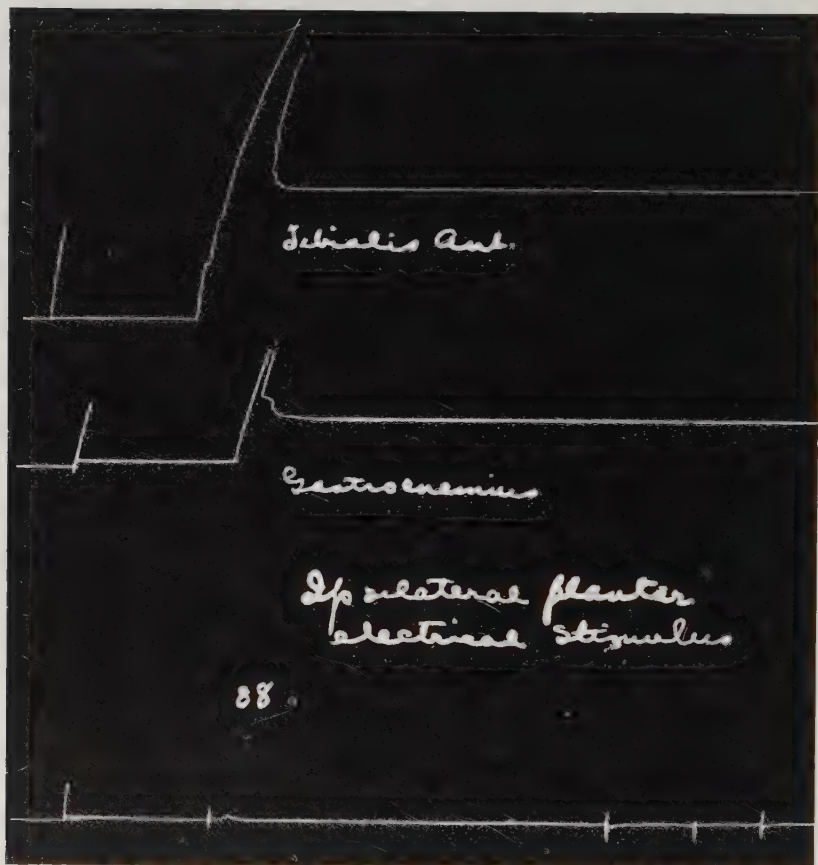


FIG. 147. Cocontraction resulting from electrical stimulation of ipsilateral planta in a spinal animal.

both tendons and counterweighting the slightly stretched muscles. The absence or resistance to contraction may well change the character of the muscle contraction. Our results may be tabulated under three headings: spinal animals, decerebrate animals and decerebro-cerebellate animals.

The spinal animals were studied for the purpose of orienting ourselves as to technic and only an ipsilateral sensory stimulus was used. Cocontraction occurred in the tibialis anticus and gastrocnemius

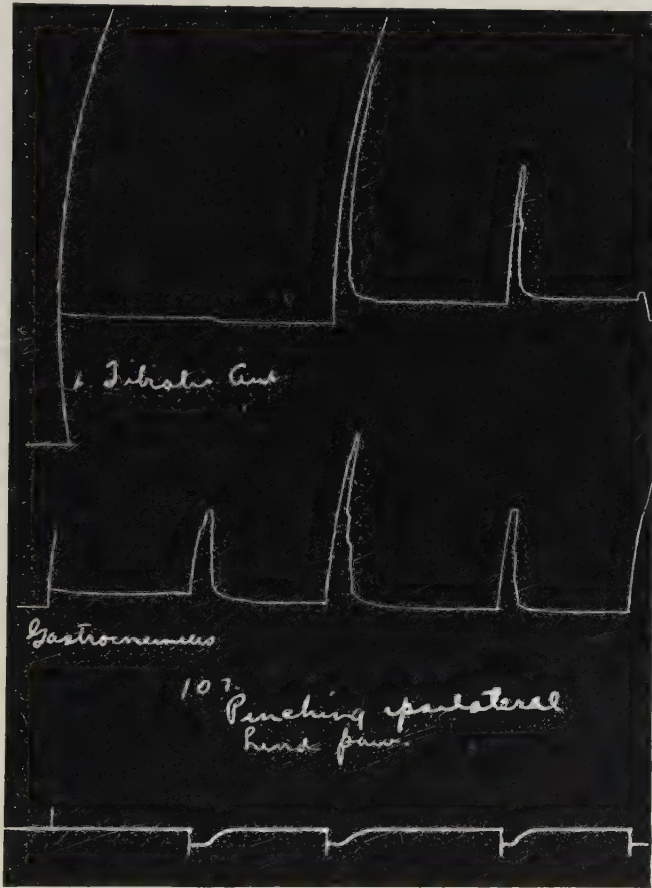


FIG. 148. Cocontraction resulting from pinching ipsilateral hind paw in a Sherrington preparation.

muscles both on pinching the hindpaws with the fingers or forceps and stimulating the planta or a cutaneous sensory nerve with an induced current (figs. 146 and 147).

Decerebrate animals, whether produced by the anemic method or a

saw, showed cocontraction upon ipsilateral stimulation of the paw by pinching or electrical stimulation of the planta, or of a sensory cutaneous nerve (figs. 148, 149 and 150).

The influence of the labyrinthine tonic reflexes upon the strength of phasic reflexes is illustrated, where when the head was turned vertex down and extensor tone increased, the amplitude of the contraction of the muscles was heightened (fig. 151).

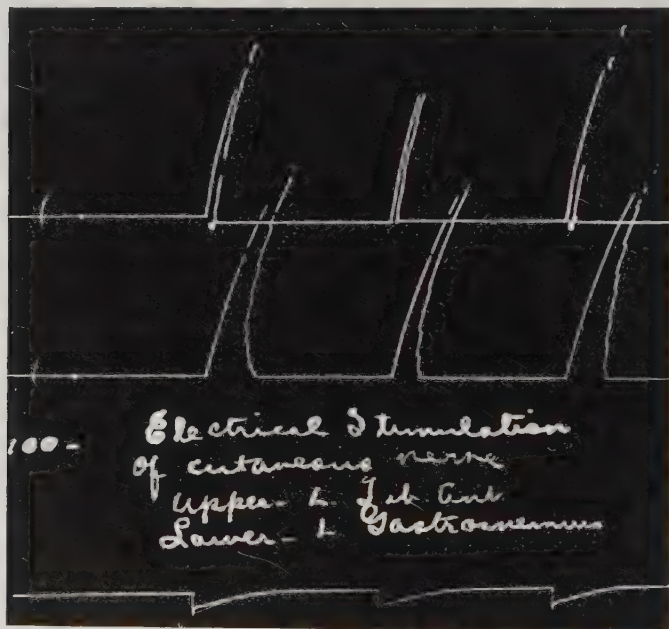


FIG. 149. Cocontraction elicited by electrical stimulation of ipsilateral sensory cutaneous nerve in a Sherrington preparation.

When the distribution of tone was flexor in character, simultaneous contraction did not occur in the opposing extensor (fig. 152).

When the head of a decerebrate animal lying on its left side was turned vertex down a contraction of the extensor resulted, and when relaxation in the extensor ensued there was an increment of tone in the flexor. When the head was turned vertex to the right a simultaneous contraction occurred in antagonistic muscles as the result of a nontonic reflex; then, as the biceps continued the contract the triceps

relaxed (fig. 153). At times such an initial contraction slightly preceded the contraction of the biceps.

It was observed that when a tonic reflex was evoked by turning the head and subsequently a reflex elicited which would produce a contraction of the opposing muscle, reciprocal innervation was the rule. Figure 154 shows an increase in tone in the triceps when the head is

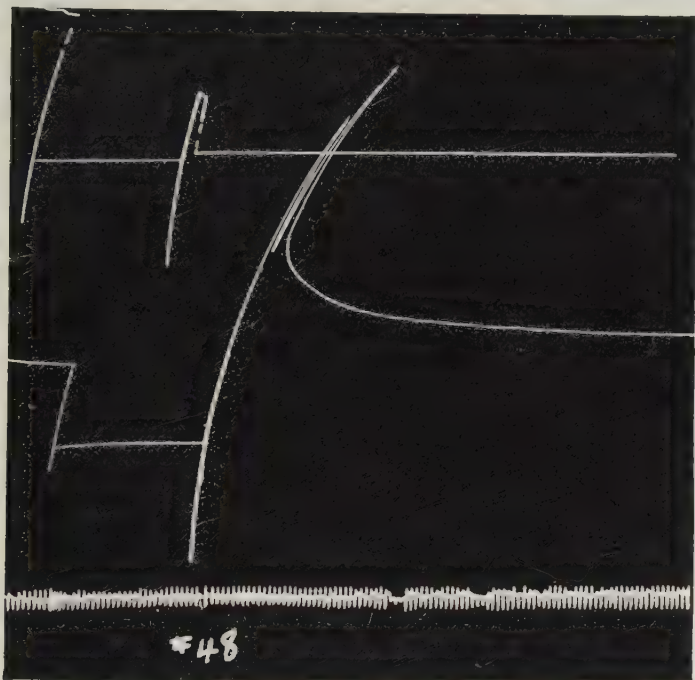


FIG. 150. Cocontraction elicited by pinching ipsilateral hind paw in an anemic decerebrate animal. Upper tracing, quadriceps; lower tracing, biceps. Abscissae were drawn on the drum.

turned vertex down; now, when the ipsilateral forepaw is pinched a contraction occurs in the biceps and a simultaneous relaxation in the triceps is seen. It will be noted that the levers are not directly superimposed by the abscissae were made upon the drum (fig. 154).

When an increase of tone was induced by a contralateral reflex such as pinching the paw, and tone was then sustained a subsequent flexor reflex, (ipsilateral pinching) produced reciprocal innervation with

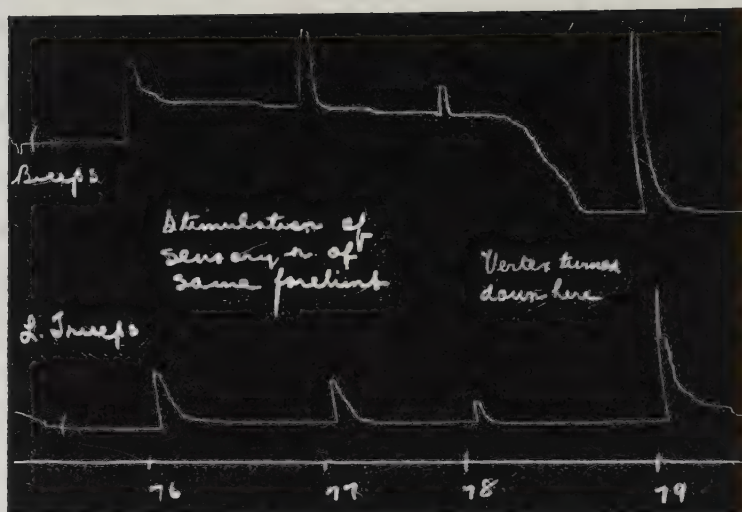


FIG. 151. Cocontraction elicited by electrical stimulation of ipsilateral sensory cutaneous nerve in a decerebrocerebellate animal. Animal lying on its left side. Upper tracing, left biceps; lower tracing, left triceps. When the vertex was turned down succeeding sensory stimulation produced marked increase in amplitude of contractions in opposing muscles.

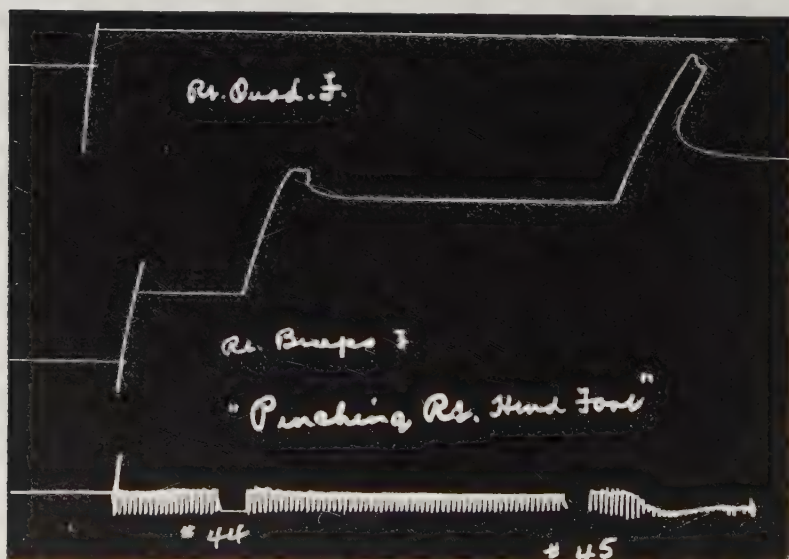


FIG. 152. Absence of contraction or relaxation in quadriceps accompanying a flexor reflex induced by pinching the right hind paw of a decerebrate animal when the tone was flexor in character.

simultaneous relaxation in the biceps. This reaction is similar to the preceding one and illustrates the effect of phasic reflexes upon tonic ones (fig. 155).

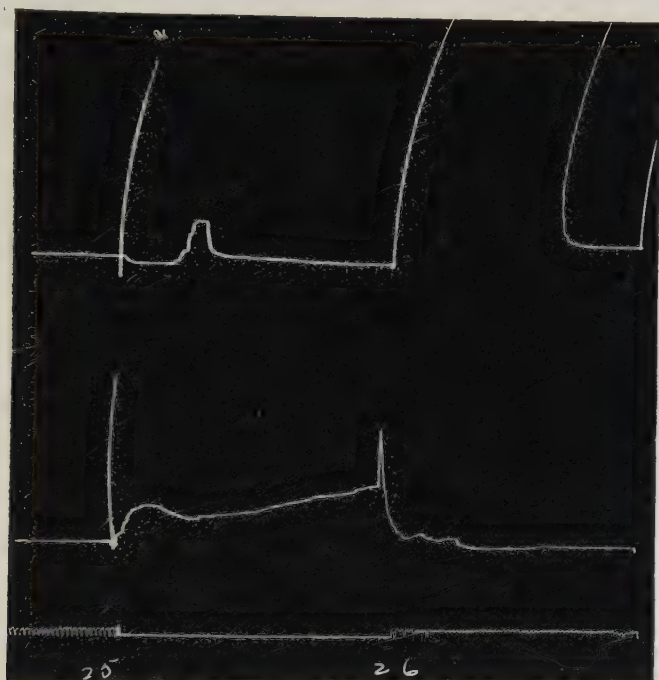


FIG. 153. Decerebrate animal lying on its left side. Upper curve, biceps; lower, triceps. In experiment 25 when the head was turned vertex down a contraction of the triceps resulted. When relaxation ensued an increment of tone was noted in the biceps. In experiment 26 cocontraction in antagonistic muscles resulted when the head was turned with the vertex to the right. As the increase of tone continued in the biceps, there was relaxation in the triceps. The cocontraction resulted from a nontonic and the reciprocal innervation from a tonic reflex.

Reciprocal innervation was constantly observed in contralateral reflexes elicited by electrical stimulation of a sensory cutaneous nerve; but when a strong current was used cocontraction occurred in the same muscle preparation (fig. 156). Similar reciprocal innervation resulted from pinching the contralateral paw (fig. 157), but when a preparation

showed extreme extensor tone, in some instances cocontraction occurred (fig. 158).

Removal of the cerebellum produced no change in the functional relation of antagonistic muscles nor in the character of the reflex patterns. Cocontraction occurred in reflexes elicited by ipsilateral nociceptive stimuli (fig. 159). When the medial side of the paw was pinched the tibialis anticus showed a marked contraction whereas the gastrocnemius showed a small one (fig. 160, *a*), when now the lateral side was pinched the amplitude in the gastrocnemius was increased

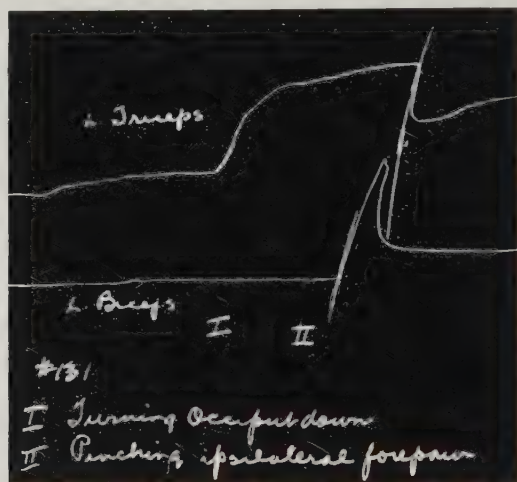


FIG. 154. Sherrington preparation. Upon turning the vertex down an increment of tone was observed in the triceps. When at *II* the ipsilateral forepaw was pinched, a contraction in the biceps occurred with a simultaneous relaxation in the triceps. Abscissae were drawn upon the drum.

(fig. 160, *b*). When now the head was turned vertex up so that flexor tone predominated, very slight contraction occurred in the gastrocnemius, and when the tibialis anticus relaxed an increment of tone was seen in the gastrocnemius (fig. 160, *a*, *b*, and *c*).

Our attention was next directed to the influence of the cerebellum as a whole upon tonic labyrinthine reflexes.

Decerebrate rigidity affords a background against which changes in tone may be readily studied. The influence of the cerebellum as a whole upon the development, degree and distribution of decerebrate

rigidity has been investigated by many workers. Sherrington (5) in 1898 noted that the rigidity persisted after ablation of the cerebellum. Despite the opposing observations of Weed (6), the work of Magnus and De Kleijn (7) and Beritoff (8) has demonstrated that decerebrate rigidity persists after ablation of the cerebellum and that

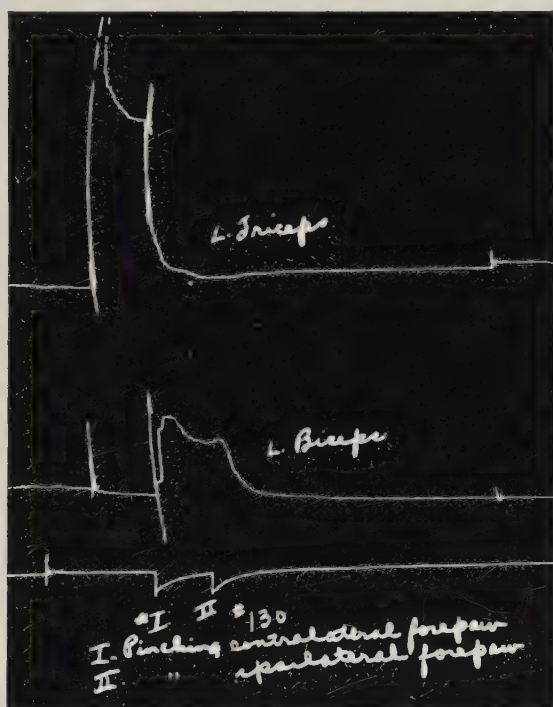


FIG. 155. Sherrington preparation. *I*, pinching contralateral forepaw produced a contraction in the triceps and no movement in the biceps. A flexor reflex was induced by ipsilateral pinching at *II* and produced simultaneous relaxation in the triceps. Abscissae were drawn upon the drum.

labyrinthine righting and tonic reflexes do not disappear after such a procedure.

Naturally, it does not follow that in an intact central nervous system the labyrinthine reflexes may not be influenced by the cerebellum. Magnus (9) believes that at some time it is likely that it will be shown that impulses from the cerebellum traveling to the brain stem centers

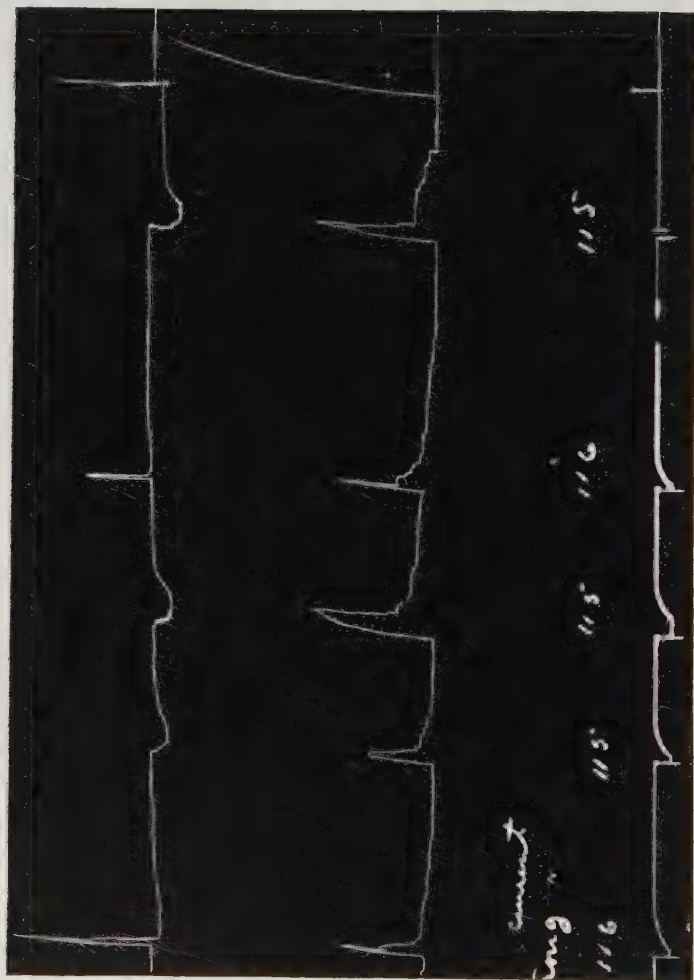


FIG. 156. Sherrington preparation. Reciprocal innervation observed upon a reflex elicited by electrical stimulation of a contralateral cutaneous sensory nerve (115). When a strong stimulation was applied cocontraction resulted (116). Upper tracing is tibialis anticus; lower, gastrocnemius tendon.

either inhibit or augment labyrinthine reflexes. In support of this he quotes the work of Bauer and Leidler, in which destruction of the vermis was followed by an increase of the "Augendrehsreaktion."

We propose to prove that the cerebellum as a whole inhibits in a general way tonic labyrinthine reflexes. As is well known, an animal decerebrated either by ablation of the cerebrum, section of the brain stem or by the anemic method (Pollock and Davis (10)) develops rigidity in all four extremities and retains indefinitely the position imposed upon it by passive movements of the head. The head is

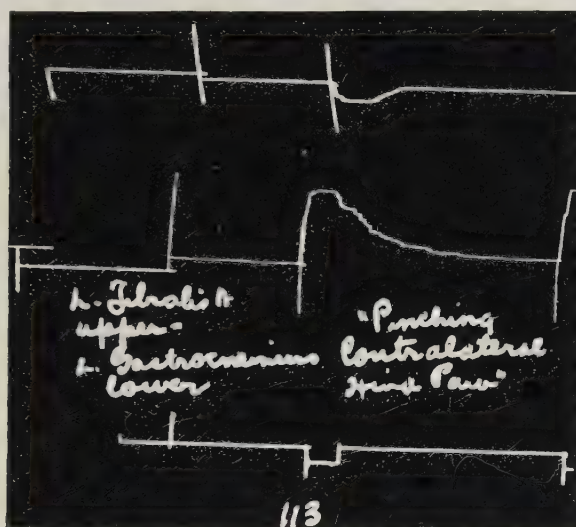


FIG. 157. Reciprocal innervation elicited by pinching contralateral hind paw in a Sherrington preparation.

kept lifted against gravity and the chin is tilted upward. When a decerebrate animal's head is immobilized in relation to the body, or is so placed that the vertex is down and the line of the mouth is at an angle of 45 degrees with the horizontal the rigidity reaches its maximum. With the vertex up and the line of the mouth 45 degrees below the horizontal the rigidity is at its minimum. When now the labyrinths are destroyed change of position of the head in relation to space produces no change in the distribution of tone. Such a change, then, is due to the labyrinthine tonic or standing reflexes. With the animal lying on its side the head is slightly extended backward, but

we have never observed the opisthotonus, which we will later describe, which occurs upon removal of the cerebellum.

Twenty-five animals were decerebrated by the anemic method to study the influence of the cerebellum upon the labyrinthine tonic reflex. Animals decerebrated by a saw or a Sherrington preparation are unsuitable for such study because of hemorrhage and shock. The

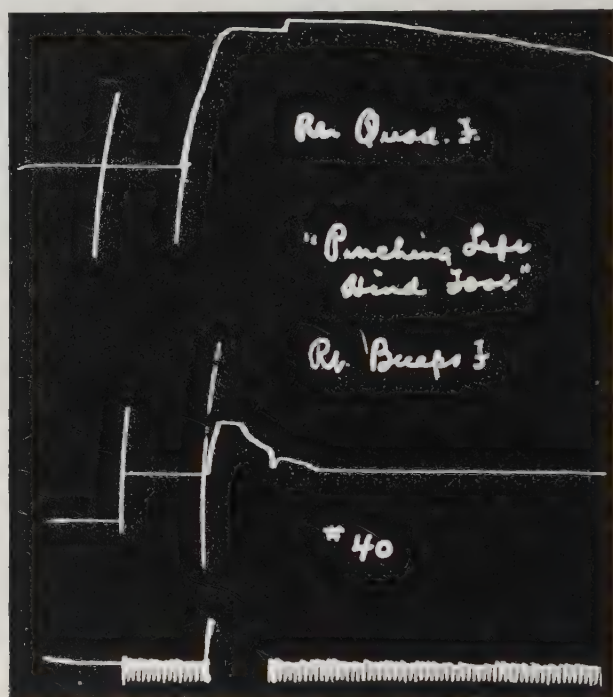


FIG. 158. Cocontraction elicited by pinching contralateral hind paw in an anemic decerebrate animal which showed extreme extensor tone.

cerebellum was removed piecemeal in some, but in most instances the posterior-inferior cerebellar arteries were either tied, coagulated or cut. The superior cerebellar arteries were already anemic because of the ligature upon the basilar and carotid arteries. The results were uniform in all animals.

Such a decerebro-cerebellate animal showed a continuous persistence of the rigidity produced by the anemic decerebration. Labyrinthine

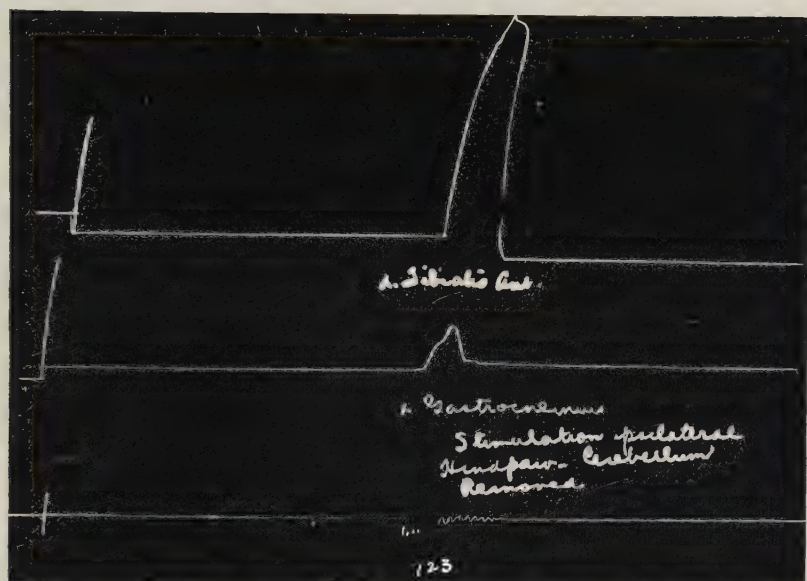


FIG. 159. Sherrington preparation with the cerebellum removed. Cocontraction elicited by electrical stimulation of ipsilateral hind paw.

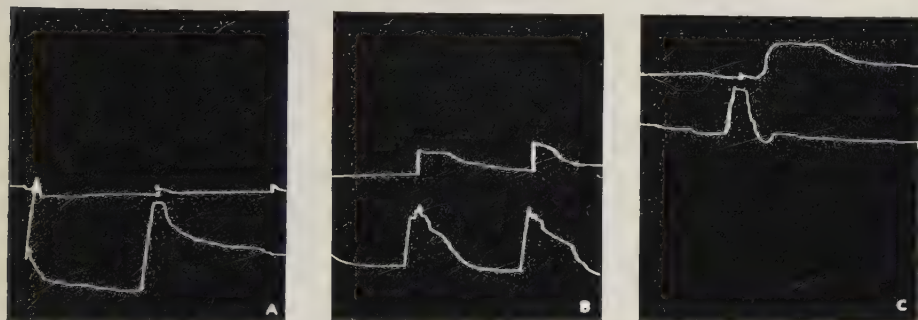


FIG. 160. *a*, Cocontraction elicited by pinching medial side of ipsilateral paw in an anemic decerebrocerebellate animal. *b*, Increase of contraction of gastrocnemius with cocontraction elicited by pinching lateral side of ipsilateral paw of the same animal. *c*, Reciprocal innervation producing contraction of gastrocnemius when the tibialis anticus relaxed following a contraction resulting from pinching ipsilateral paw, with flexor tone predominating in the same animal. Upper tracing, gastrocnemius; lower, tibialis anticus.

and neck tonic reflexes were present. When the head of an ordinary decerebrate animal, lying on its side was turned vertex down an increase in tone was observed. It occurred relatively slowly and smoothly. When the head of a decerebro-cerebellate animal was turned vertex down, the forelegs were thrust forward suddenly with great force and with unsheathing of the claws. The force of this tonic contraction was so great that often the whole body was displaced. Its sudden appearance was tetanic, startling, and entirely dissimilar to anything observed in an ordinary decerebrate preparation. The rigidity in the extremities was so marked that passive flexion could be performed only by the greatest force (fig. 161).



FIG. 161. Exaggerated labyrinthine tonic reflex in a decerebrocerebellate animal.

Immediately following removal of the cerebellum the head assumed an attitude of extreme opisthotonus. When it was passively flexed the rigidity in the extremities, the forelegs especially, diminished and a position of semiflexion was assumed. When the head was released it slowly assumed the original position of opisthotonus with accompanying extreme extension of the forelegs. If the animal was then turned on its back the markedly retracted head rested on its frontal pole and the chin was in a line extended from the neck. The animal could then be balanced in this position, which would be retained indefinitely. When placed upon its abdomen with the extended forelegs hanging over the edge of the table the marked retraction of the head persisted unchanged (fig. 162).

Extreme opisthotonus has been described by Bazett and Penfield (11) in certain decerebrate animals immediately after operation and was generally accompanied by tonic fits in which the rigidity underwent extreme accentuation. In these animals the respiration was usually slow (though occasionally there was a fast and shallow respiration). Bazett and Penfield say that this condition is seen in animals with evidence of postoperative hemorrhage, and that as a rule blood is found below the tentorium.

The degree of opisthotonus which we have described in decerebro-cerebellate animals has never been observed by us in ordinary decere-



FIG. 162. Opisthotonus resulting from removal of cerebellum in a decerebrate animal.

brate animals. It was not due to hemorrhage or other injury to subtentorial structures, as will be seen from the following observation. When the labyrinths were destroyed in such an animal no change in tone was observed when the head was turned vertex down, and the opisthotonus entirely disappeared. From this we conclude that the cerebellum as a whole inhibits tonic labyrinthine reflexes which are responsible for the production of the marked increase in rigidity when the head is turned vertex down and for the extreme opisthotonus.

Opisthotonus, or under certain conditions emprosthotonus, has long been known to occur as the result of experimental lesions in the cerebellum. These phenomena have been attributed by Ingvar (12)

to lesions specifically of the vermis. The disappearance of opisthotonus after destruction of the labyrinths proves that this change in posture is due to labyrinthine tonic reflexes. Our results, therefore, offer an explanation of the inhibition of decerebrate rigidity found by some investigators upon stimulation of the cerebellar cortex, underlying structures, or the superior cerebellar peduncles. (Miller and Banting (13), Cobb, Bailey and Holtz (14).)

DISCUSSION

Cocontraction and reciprocal innervation both occur as the result of reflex activity depending upon the particular function to be served. Schoen (15) in describing the "stutzreaktion" in the forelegs notes simultaneous contraction of antagonistic muscles when fixation of joints was the purpose of the reflex. Pritchard (16), describing the same reflex in the hindlegs, showed that when stretching alone was the purpose, reciprocal innervation occurred.

Ipsilateral nociceptive stimuli produced cocontraction in spinal, decerebrate, and decerebro-cerebellar animals.

Contralateral nociceptive stimuli produced reciprocal innervation except when very strong stimuli were used, or when the muscle opposed to that one whose contraction the reflex evoked was in a state of heightened tone.

Nontonic reflexes from the neck accompanying tonic ones produced a simultaneous contraction in the antagonistic muscle, which immediately relaxed and continued to relax during the heightened tone of the agonist.

Phasic reflexes inhibiting tonic ones produces reciprocal innervation.

The distribution of tone as modified by neck and labyrinthine reflexes determined the degree of functional interrelation of muscle contractions produced by phasic reflexes and at times prevented any activity in the opposing muscle.

When cocontraction occurred as the result of an ipsilateral nociceptive stimulus and the increase in tone was sustained by a tonic reflex in one of the muscles, the antagonist contracted as that muscle relaxed.

Removal of the cerebellum did not affect the functional interrelation of muscular contractions resulting from tonic and certain phasic reflexes.

It is evident that these observations cannot be used to determine the behavior of antagonistic muscles in voluntary movements.

Removal of the cerebellum in a decerebrate animal produced a state in which the labyrinthine tonic reflex evoked by turning the vertex down was markedly increased.

A degree of opisthotonus unobserved in ordinary decerebrate animals occurred in the decerebro-cerebellate animals. The opisthotonus disappeared after destruction of the labyrinths.

CONCLUSIONS

1. The cerebellum does not modify the functional interrelation of muscular contractions resulting from tonic and certain phasic reflexes.
2. The cerebellum as a whole inhibits in a general way the tonic labyrinthine reflexes.

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CHAPTER XIV

THE EFFERENT CONNECTIONS OF THE CEREBELLAR CORTEX; INVESTIGATIONS BASED UPON EXPERI- MENTAL EXTIRPATIONS IN THE CAT¹

LESLIE B. HOHMAN, M.D.

THIS report is a summary of experiments upon the cerebellar cortex in a series of cats. The attempt was made to remove small portions of various parts of the cerebellar cortex, under rigid asepsis, and great care was exercised not to damage any underlying central white matter or central gray matter. The brains of animals, sacrificed after two to three weeks, were stained with osmic acid by the Marchi-Busch technique, and the degenerations were then studied in serial section.

Although it was found that, even with great care, more extensive damage resulted to the cortex than was planned, nevertheless, a series of seventeen animals was successfully obtained which fulfilled the following conditions: first, none of the brains shows any damage to underlying central white or gray matter; secondly, every portion of the cortex, with the exception of the flocculus, was so injured that consequent degenerations could be studied as relatively isolated pathways.

I have selected three experiments to present in this summary because they show the essential results of the study, although the complete proof can only be obtained from the whole series.

Before proceeding with these experiments, I shall first briefly review the main features in the anatomical organization of the cerebellum. This organ develops in intimate relationship with the middle hind-brain segment and more particularly with the vestibular nuclei. It is covered by a uniform cortex, which in turn covers a great mass of white matter in whose depths is embedded a group of paired nuclei—these nuclei forming a crescent partly surrounding the ventricle.

Of these central gray masses, the roof nuclei are intimately con-

¹ From the Neurological Laboratory of the Henry Phipps Psychiatric Clinic, Johns Hopkins Hospital.

nected with the vestibular nuclei by direct and crossed afferent and efferent pathways.

The large mass of afferent pathways, however, to the cerebellum, are to the cortex and comprise the following:

1. By way of the inferior cerebellar arm or corpus restiform afferents are conducted to the vermis cortex, probably to both sides. In this inferior arm are to be found the direct spino-cerebellar tract (Fleschig's), the olivo-cerebellar connections (from the opposite olive to the vermis, after the olive has relayed fibers from the thalamus, by means of the thalamo-olivary tract), fibers from the homolateral and contralateral posterior column nuclei, and probably also pathways from the homolateral lateral nucleus, and the homolateral tegmentum.

2. By means of the middle cerebellar arm, the pons, afferents are conducted to the hemisphere cortex of the cerebellum, from the opposite cerebral hemisphere. These connections are relayed in the pons nuclei, but are probably all crossed.

3. A further afferent vermis cortex connection is made with the spinal cord through the indirect spino-cerebellar tract (Gowers).

The efferents from the central nuclei leave the cerebellum by two main pathways.

1. The roof nuclei-vestibular connections, direct and crossed.

2. The dentate- (and probably the intermediate cell mass-globosus and emboliform) rubro-thalamic tract, by way of the decussating superior cerebellar arm or brachium conjunctivum.

The cerebellar cortex sends its efferents, by means of the Purkinje fibers, down to the central grey masses, which are relay stations to the final efferent cerebellar pathways. Now this cerebellar cortex, is made up of (1) a central strip called the vermis, which, together with two small ventral lateral tufts of cortex, the flocculli, represent, phylogenetically, the older part of the cortex; (2) the cerebellar hemispheres which lie between the vermis and flocculli, and develop, phylogenetically, as the cerebral cortex increases.

It is especially important to indicate the manner in which this cerebellar cortex makes its connections with the central grey masses, as well as what other connections it establishes in addition to those of cerebellar nuclei.

Two previous studies on the cerebellar cortex must be considered: Horsley and Clark (1) in 1905, and Saito (2) in 1923-1924. Horsley and Clark's work can be summarized as follows:

1. The efferent terminations of the Purkinje cells are all ipsilateral and each portion of the cortex sends its fibers to the nearest underlying nuclear mass.

2. There are no direct efferents from the cerebellar cortex to the midbrain, pons, medulla or spinal cord.

These authors did, however, note a connection with the vestibular nucleus in very extensive lesions.

3. No association fibers extend across the midline.

4. Arcuate interfolial fibers do not extend more than two or three folia.

The experimental study by Horsley and Clark was made upon cats, dogs, and monkeys.

Saito, in Marburg's laboratory, who worked only with rabbits, agrees in the main with Horsley and Clark but finds contrary results on some scores.

1. He subscribes to the simplicity of arrangement of connections between cortex and nuclei, but does not subscribe to the strict ipsilaterality of connections. He found each side of the vermis connected with the nuclei of both sides (excluding the dentate).

2. He also finds no efferents to the spinal cord, but did find (a) an ipsilateral pontine connection with the parafloccular mass (lobus petrosus), (b) widespread vestibular connections with the ipsilateral and contralateral vermis, (c) slight connections of the hemispheres to the superior cerebellar arms.

3. He found extensive association systems from one hemisphere to the other through the superior and inferior commissures, and also extensive connections from the vermis to all parts of the hemispheres except the paraflocculus.

Our results agree in very large part with those of Horsley and Clark, and we can subscribe to none of the disagreeing results reported by Saito, except partly on the score of vestibular connections. We bear in mind that Saito worked exclusively with rabbits, but we wish to point out that the osmic acid method is a very dangerous one, and if one is not cautious to select rigidly controlled experiments, results may be unreliable. For unknown reasons some specimens do not stain at all, while others overstain and show evidences of degeneration where none exists. Degenerations are to be regarded as valid only if definite areas of cortical degenerations begin the staining, and that the pathway be continuous from this. Dust-like precipitations must not be taken as evidence of degeneration.

My results are best presented as a series of sections taken from three selected experiments.

RESULTS OF EXPERIMENT INDICATED AS CAT NO. 5

From a view of the whole brain it appears that there is a bilateral lesion of the anterior vermis. A section (5-8-9) through the lesion shows the surface vermis cortex degenerated, and a mass of degenerated fibers in the immediately subjacent white matter of the corresponding folia. A section taken slightly posterior (5-8-5) shows this same degeneration split into two sets of three bundles lying on either

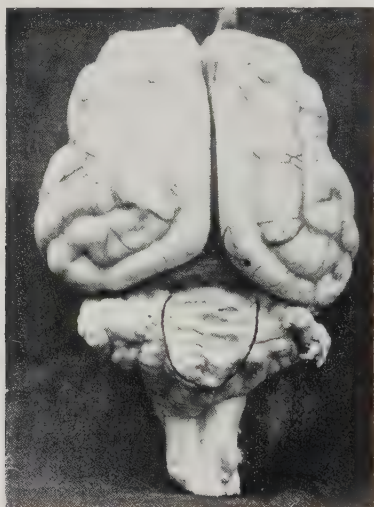


FIG. 163. Cat 5. Cerebellum before sectioning. Lesion outlined, showing damage to the anterior vermis.

side of a clear zone in the midline. The more mesial (*A-V-F*) is flat and clearly separated from a medial bundle (*A-V-D*), while laterally there is a large less compact bundle (*A-V-I*). If one examines a more caudal section posterior, just at the caudal end of the anterior vermis (5-7-9), these three bundles can still be seen in clear isolation. The mesial bundle, *A-V-F*, is about to terminate in the ipsilateral roof nucleus, the middle bundle, *A-V-D*, is directed somewhat vertrally and lies just medial to the intermediate cell mass (globosus and emboli-

form) and the lateral bundle *A-V-I* is being split by the unstained bundles of the restiform body.

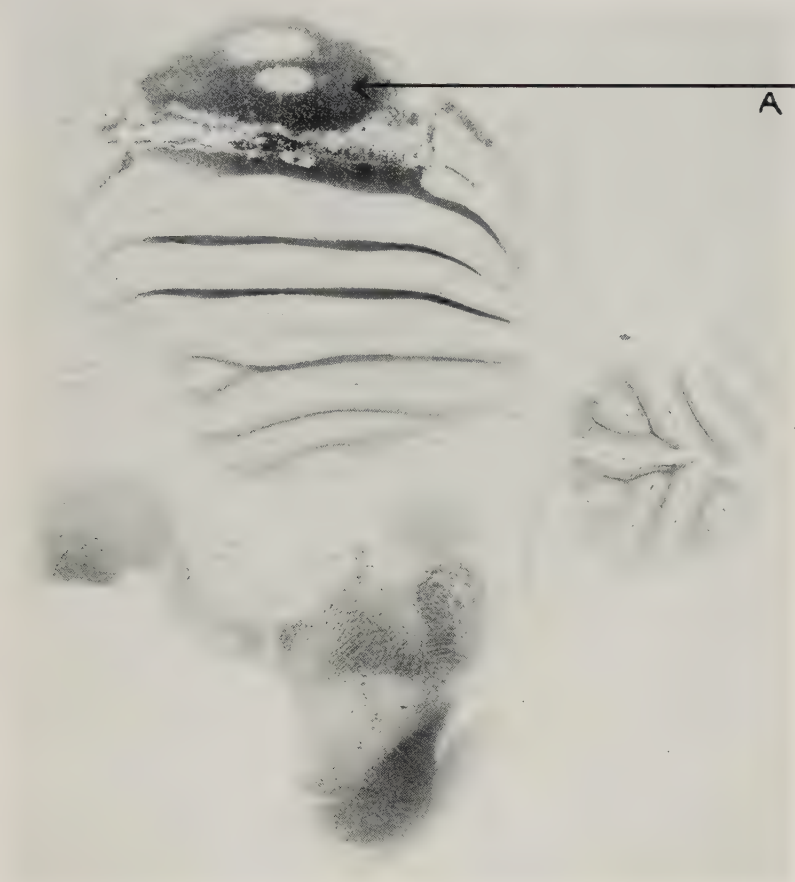


FIG. 164. Section 5-8-9. Through the inferior colliculus, and anterior vermis. *A*, degenerated cortex of anterior vermis.

N. B.: All sections are reversed in mounting and, consequently, in the photographs. The actual right side shows on the left side of the page.

Finally in a section (5-7-4) still more caudally through the hind-brain segment, is seen the termination of these three anterior vermis

group of efferents. The mesial bundle *A-V-F* has practically exhausted itself in the ipsilateral roof nucleus. (It should be noted

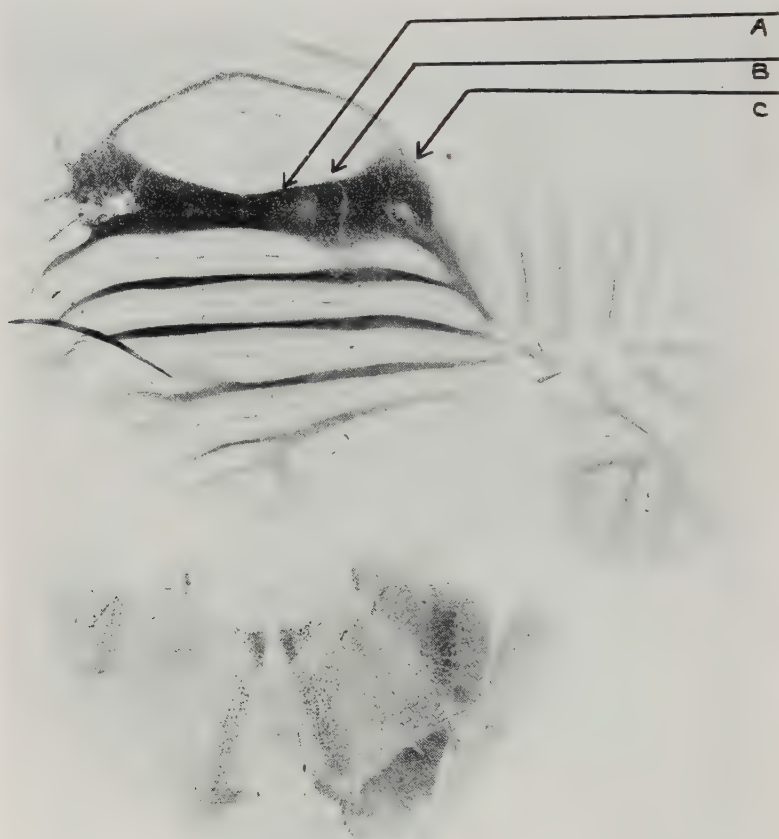


FIG. 165. Sections 5-8-5. Through the hindbrain and anterior vermis. *A*, anterior vermis—roof nucleus bundle (*A-V-F*); *B*, anterior vermis—Deiters' nucleus bundle (*A-V-D*); *C*, anterior vermis—intermediate cell mass bundle (*A-V-I*).

that everywhere through the series, there is a clear zone of separation between the roof nuclei, and no evidence of any degenerations suggest-

ing any decussation across the midline); the bundle *A-V-D* is now terminating in Deiter's nucleus of the same side; and, finally, the lateral bundle is terminating in the intermediate cell mass of the same side.

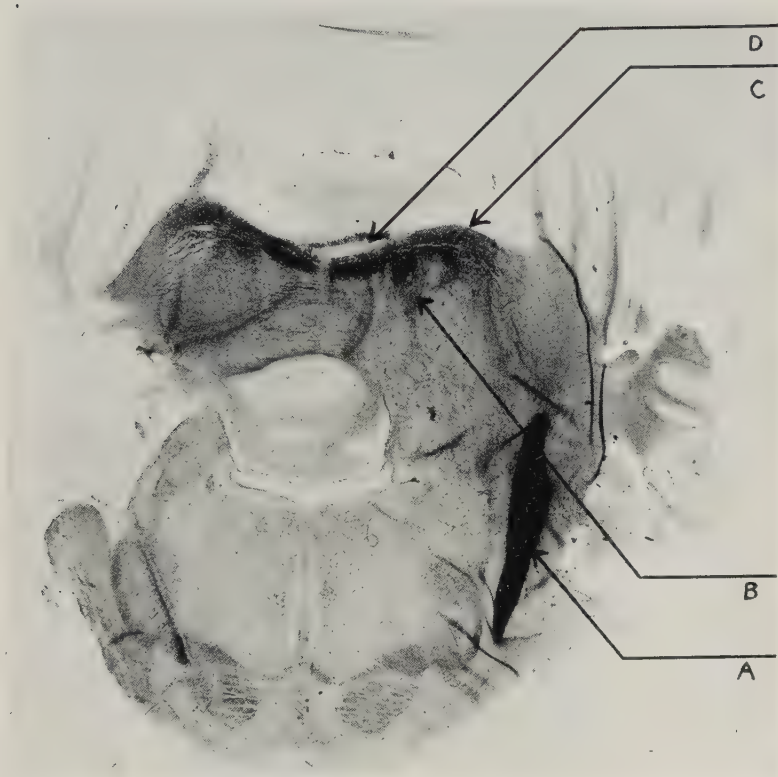


FIG. 166. Section 5-7-9. Through the hindbrain (caudal to 5-8-5). *A*, adventitious staining; *B*, anterior vermis—Deiter's nucleus bundle (*A-V-D*); *C*, anterior vermis—intermediate cell mass bundle (*A-V-I*); *D*, anterior-vermis roof nucleus bundle (*A-V-F*).

These facts indicate that the anterior vermis makes only ipsilateral connections; that there is a radial like arrangement of connections on either side of the midline connecting the one side of the vermis with the roof nucleus, Deiter's nucleus, and the intermediate cell mass.

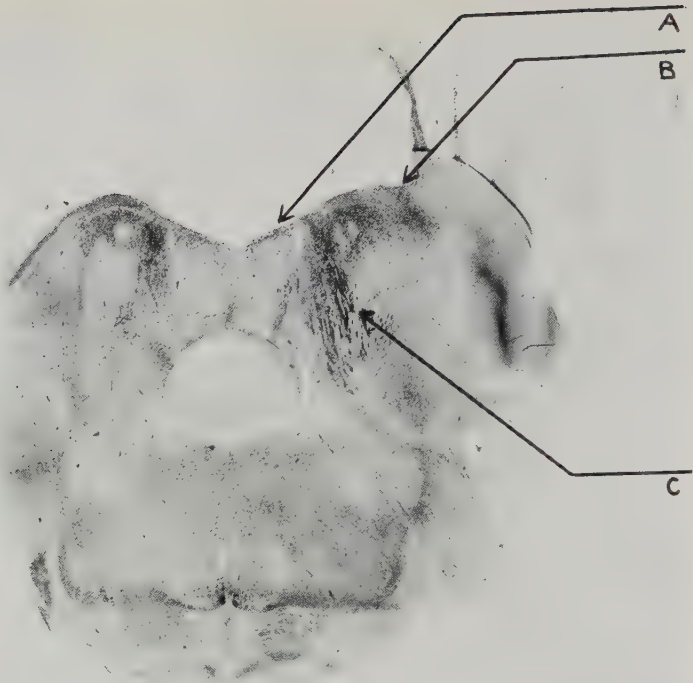


FIG. 167. Section 5-7-4. Through the hindbrain (caudal to 5-7-9). *A*, final terminations of the *A-V-F* bundle; *B*, termination of *A-V-I*; *C*, termination of *A-V-D* in Deiter's nucleus.

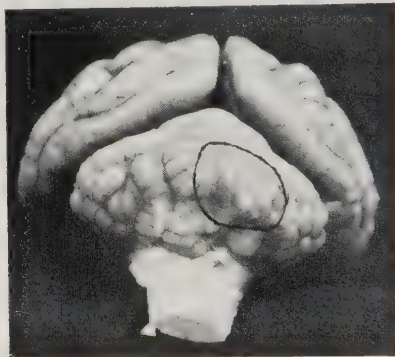


FIG. 168. Cat 30. Cerebellum before sectioning. Lesion outlined, showing involvement of inferior curved vermis, right lobus simplex, right crus *I*, right crus *II*, and right paramedian lobule. Damage to the parafofculus is present but not visible.

Further there is no evidence of pons, midbrain, or spinal cord connections. There is furthermore no evidence of any degenerations to either cerebellar hemisphere or to the posterior vermis.

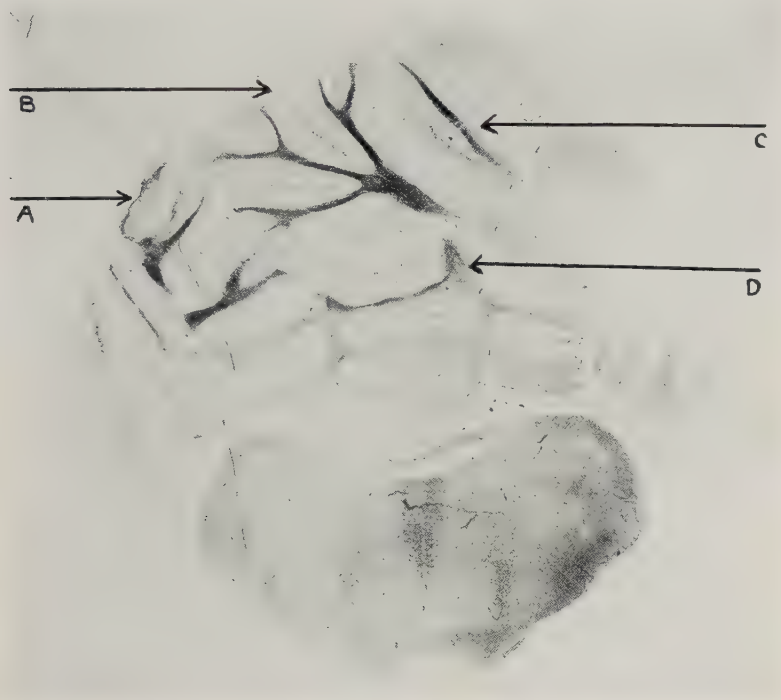


FIG. 169. Section 30-4-2. Through the hindbrain, inferior vermis, paramedian lobules, crus *II*, and paraflorcular masses. *A*, degenerated cortex of right paramedian lobule; *B*, degenerated cortex of the inferior curved vermis; *C*, clear zone separating the right and left halves of the curved vermis degenerations; *D*, lobus simplex—inferior vermis association bundle (*L-S-I-V*).

RESULTS OF EXPERIMENT INDICATED AS CAT NO. 30

The photograph shows a lesion of the posterior vermis (anterior portion, mainly curved inferior vermis) a bit of lobus simplex or middle lobe, the medial portion of the right ansiform lobe (crus *I* and crus *II*), and the right paramedian lobe. This experiment demonstrates connections of the curved portion of the inferior vermis clearly.

A section taken through the hindbrain and the inferior curved vermis as well as both paramedian lobules (30-4-2) shows definite cortical damage in the surface curved inferior vermis, and also in the upper folia of the right paramedian lobule. These surface degenerations are sending degenerated fibers into the immediately subjacent white matter of the same folia, and, in addition, one can observe in the

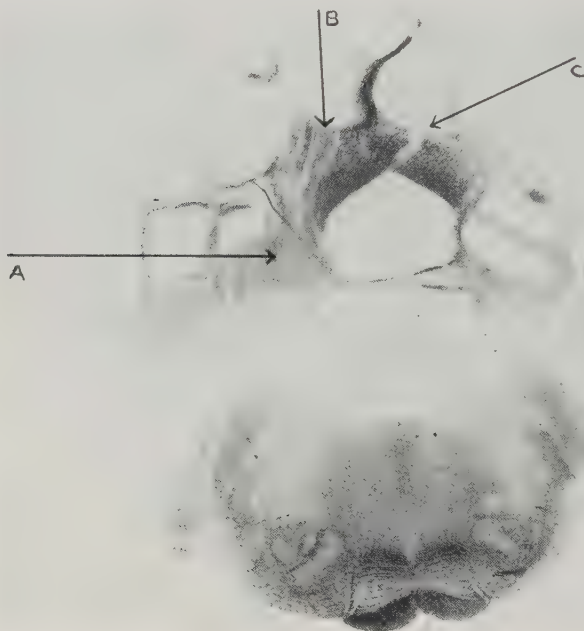


FIG. 170. Section 30-5-4. Through the middle hindbrain segment, the junction of the inferior curved vermis and lobus simplex, and left paramedian. *A*, efferent degenerations of the paramedian lobule; *B*, the lobus simplex inferior vermis association bundle; *C*, clear zone separating the degenerations of the two halves of the inferior vermis.

lowermost strands of white matter of the inferior vermis (pyramis) two bundles of degenerations on both sides of the midline. These are not the result of inferior vermis degenerations, but are derived from cortical damage in the lobus simplex (middle lobe). One can also see that the bands of degenerations are clearly separated in the midline. The more lateral bundle of these association fibers, terminates

in the ipsilateral paramedian lobule, and inferior portion of the inferior vermis (*L-S-I-V*) by way of a connecting strand of white matter between the inferior vermis and the paramedian lobule. There are, however, no efferent fibers from the paramedian which connect through this same band.

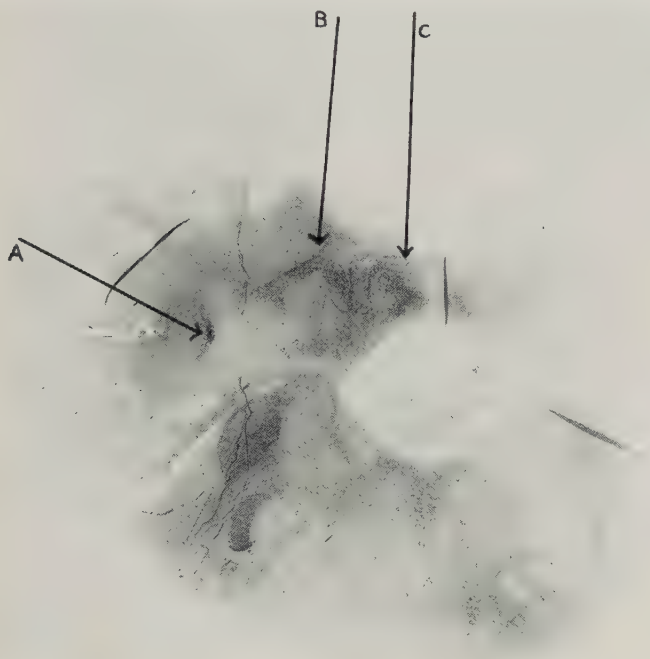


FIG. 171. Section 30-6-2. Through the hindbrain segment, with all central gray masses (dentate, intermediate cell mass, and roof nucleus) visible. *A*, termination of paramedian lobule degenerations; *C*, termination of right half of inferior vermis and right half of the vermis portion of the lobus simplex.

A section (30-5-4) taken more cephalad through the hindbrain segment, showing the upper end of the inferior curved vermis, the upper end of the left paramedian, the two paraflorculus masses, and the right crus *II*, gives important degenerations. On either side of the midline there is a bundle of degenerations, clearly separated by a clear zone. These are made up of degenerated fibers from the



FIG. 172. Cat 21. Cerebellum before sectioning. Lesion outlined, showing involvement of right half of the anterior vermis, right half of lobus simplex, right paramedian, right crus *I*, crus *II*, and right paraflocculus mass.

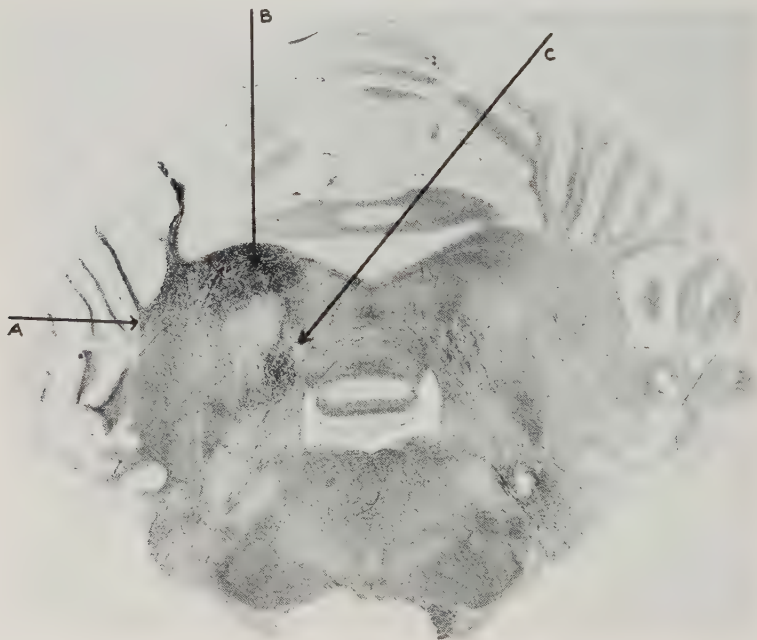


FIG. 173. Section 21-6-5a. Through the hindbrain segment, posterior end of the anterior vermis, anteriorly curving folia of lobus simplex, crus *I*, and paraflocculus mass. *A*, degenerations from crus *I*; *B*, anterior vermis-intermediate cell bundle (*A-V-I*); *C*, anterior vermis-Deiters' bundle (*A-V-D*).

inferior curved vermis, lying posterior and in the present section. The split between these bundles lies diagonally. This is the result of the curving of the inferior vermis. If one imagined the vermis stretched out in a straight line, one would find the same radial arrangement as in the anterior vermis, but due to its curving, the midline split between the fibers of the two sides is set at an acute angle, especially at the more curved portion of the vermis. Actually the radial ipsilateral arrangement from the inferior vermis is as strictly maintained as in the anterior vermis. Just lateral to the right central bundle one sees a long bundle of degenerations sweeping down to the lateral border of white matter which is continuous with the lateral pyramid bundle noted in the preceding section (*L-S-I-V*). This is derived from the lateral part of the lobus simplex (middle lobe). On the right, just lateral to this bundle and dorsal to the lower tip of the dentate is a mass of degeneration which are the anterior contributions of the paramedian lobule efferent degenerations. They terminate in the intermediate cell mass.

From the right paraflocculus mass, degenerations can be followed medially to the inferior lateral border of the dentate nucleus.

In a section through the hindbrain (30-6-2) and all of the central nuclei, one observes the final terminations of the inferior vermis in the ipsilateral roof nucleus (caudal half of the roof nucleus) clearly separated from the roof nucleus of the opposite side and with no evidence of any decussation fibers. Further, the termination of the paramedian lobule about the ipsilateral intermediate cell mass can be made out, and, furthermore, the degenerations of crus *I* and crus *II* can be seen on the dorsolateral surface of the dentate.

RESULTS OF EXPERIMENT INDICATED AS CAT NO. 21

The photograph of the whole brain shows a large superficial lesion but one limited very sharply to the right half of the cerebellum, except in the inferior curve vermis, where the pathway to the left roof nucleus is degenerated because the vermis curves to the right. The damage in the anterior vermis extends to the left just beyond the midline. A section just at the caudal end of the anterior lobe (21-6-5a), discloses the three bundles, noted in cat 5, *A-V-F*, *A-V-D*, and *A-V-I*, clearly visible on the right, and with the exception of a very few fibers in the left roof nucleus, corresponding to the slight damage on the left side of the anterior vermis, there is no evidence of any degenerations

anywhere on the left side of the cerebellum. There are degenerations in the anteriorly curving folia of the lobus simplex, both in the cortex and white matter, visible, as well as degenerations in crus *I*.

A section somewhat caudal to this (21-6-2a) through the hindbrain segment, the anterior vermis, anterior curving folia of lobus simplex, crus *I*, crus *II*, and paraflocculus, shows clearly the unilateral degenera-

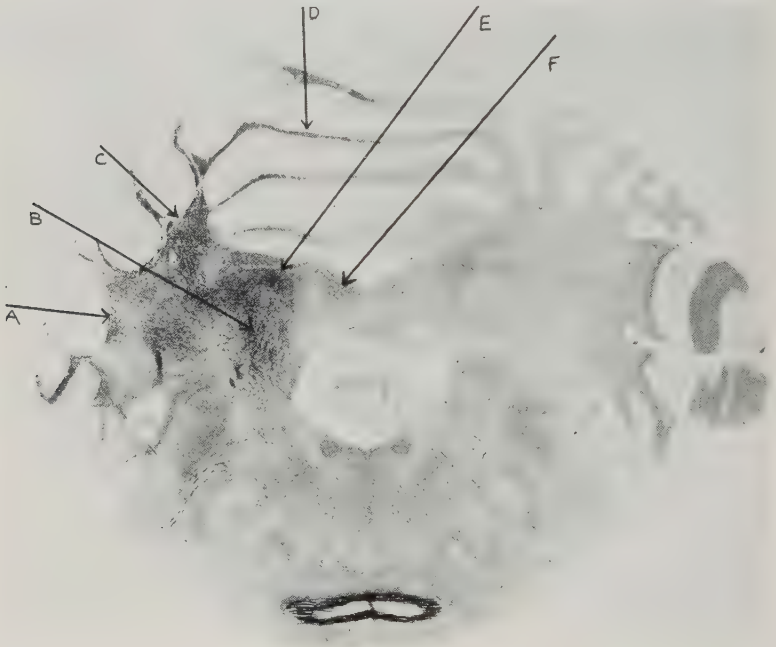


FIG. 174. Section 21-6-2a. Through the hindbrain segment (caudal to 21-6-5a). *A*, crus *II* degenerations; *B*, *A-V-D* bundle; *C*, crus *I*, and anteriorly curving folia of lobus simplex degenerations; *D*, right half of anterior vermis degenerations; *E*, *A-V-I* bundle; *F*, *A-V-F* bundle.

tions in the anterior vermis, the terminations of the right anterior vermis in the right roof nucleus (*A-V-F*), the anterior vermis Deiter's (*A-V-D*) connections, and the anterior vermis—intermediate cell mass (*A-V-I*) pathway. Furthermore, one can see the medial folia of the anterior curving portion of the lobus simplex, sending its degenerations in the intermediate cell mass, and that this mass of degenerations is clearly separated from those of crus *I* and upper

half of crus *II* which are running to the dorso-lateral border of the dentate. The lower border of the dentate is free of degenerations, showing that the ansiform lobe uses the dorsal-lateral part of the dentate, while the paraflocculus uses the ventrolateral border.

It is to be noted that the left half of the cerebellum is completely free of degenerations and that the pons contains no degenerated fibers.

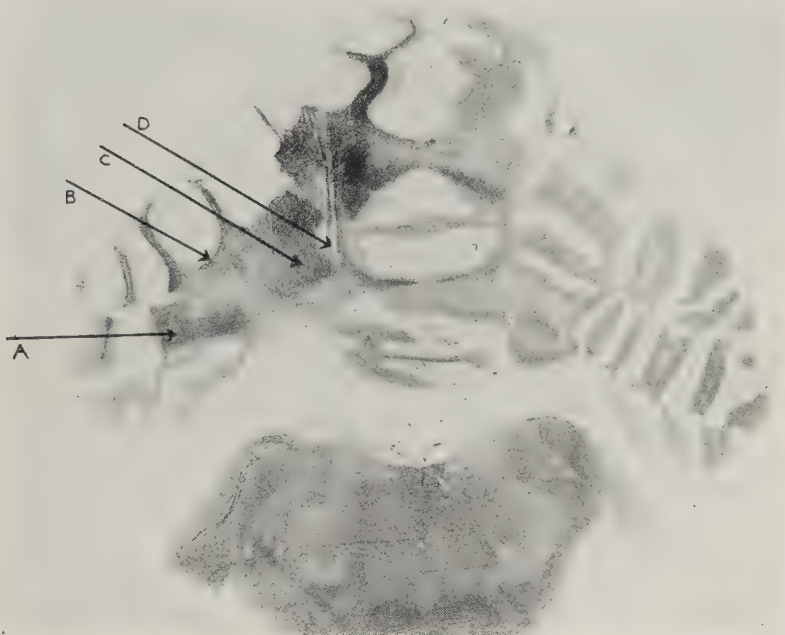


FIG. 175. Section 21-5-3a. Through the hindbrain segment; (caudal to 21-6-2a) showing the right and left paraflocculus, right and left crus *II*, inferior vermis, vermis portion of lobus simplex. *A*, paraflocculus degenerations; *B*, crus *II* degenerations; *C*, paramedian lobule degenerations; *D*, lobus simplex-inferior vermis association bundle (*L-S-I-V*) (note the absence of this bundle on opposite side).

A final section (21-5-3a) through the entrance of the eighth nerve, the inferior curved vermis, crus *II*, and paraflocculus, shows the lobus simplex-inferior vermis (*L-S-I-V*) association bundle clearly outlined on the right and its absence on the left. It demonstrates again that the ventro-lateral border of the dentate serves for the reception of the paraflocculus and the lower part of crus *II*. Another

point is to be noted, the paramedian lobule degenerations are sharply separated from those of the inferior vermis by a clear zone which has no evidence of any degenerated fibers in it.

SUMMARY

1. Each half of the anterior vermis cortex connects radially from the center to lateral border with the ipsilateral anterior half of the roof nucleus, ipsilateral Deiters, and ipsilateral intermediate cell mass.

2. The two halves of the lobus simplex efferents connect with the ipsilateral roof nuclei and intermediate nuclei.

3. Each half of the inferior vermis efferents connect with posterior half of the ipsilateral roof nucleus.

4. The efferents of the anterior curving portions of lobus simplex connects with the ipsilateral intermediate cell mass.

5. Crus *I* efferents terminate on the dorso-lateral border of the dentate.

6. Crus *II* efferents terminate on the dorso-lateral and lateral border of the dentate.

7. The paraflocculus efferents terminate on the ventro-lateral border of the dentate.

8. The paramedian lobule sends its efferents to the corresponding intermediate cell mass.

9. There is a long ipsilateral association bundle from each lateral border of lobus simplex to the inferior vermis and the paramedian lobule.

10. There are no pons, midbrain, or spinal cord efferents from the cerebellar cortex. The only cerebellar cortex efferent which leaves the cerebellum is from the Anterior vermis to Deiters' nucleus.

These results are practically at one with those of Horsley and Clarke, except that the anterior vermis Deiters' connection is definitely established along with the lobus simplex (middle lobe) posterior vermis association bundle.

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Section III

PATHOLOGICAL STUDIES OF THE CEREBEL-
LAR CONNECTIONS

CHAPTER XV

CEREBRO-CEREBELLAR AGENESIS IN ITS RELATION TO CEREBELLAR FUNCTION

LEON HASTINGS CORNWALL, M.D.

FOR the material on which this report is based I am indebted to Dr. Stanley Cobb of Boston, Massachusetts. It consisted of a "tumbling kitten" that showed evidence from birth of pronounced neural defects referable to the kinetic regulatory systems. The animal was sent to Dr. Tilney by Dr. Cobb in the summer of 1926 and after several weeks of observation, during which moving picture records were made, the animal was killed at the age of two months. At the request of Dr. Tilney I undertook the pathologic investigation of the animal's brain. This study was made under his supervision and for his helpful guidance and many suggestions I take this occasion to express my grateful appreciation.

Dr. Cobb was good enough to obtain from the erstwhile mistress of this kitten a very satisfactory life history together with data concerning the mother and maternal grandmother. I shall include this verbatim as it is a tribute to the observational acuity of its author, Mrs. W. S. Booth of Cambridge, Massachusetts:

Here are the only facts that I know about the tumbling kitten. We got his grandmother at Harvard, Massachusetts, in 1924 from a good stock of black cats. She was born June 3, 1924, and was a fine cat, intelligent, affectionate and a clever mouser.

On May 2, 1925, she had four kittens. Two were all black like herself and two were fine Maltese. They were all healthy and flourishing. We named one of the (black) females Nicolette—a nice, clean, affectionate and intelligent cat.

On April 24, 1926, Nicolette had four kittens. One was born dead. This one was very much underdeveloped—in fact hardly more than a well defined embryo. The second, a golden-yellow male, died in two days. The third, a golden-yellow female, was very lively, bright and healthy. We still have her. The fourth was the greyish mongrel male that I took to the laboratory. He was lazier than the female and opened his eyes two days later—almost ten days after birth. He was also very fat and greedy and was always first to nurse and last to stop, pushing his sister away. His laziness and fatness seemed, at first, sufficient cause for not walking or climbing as his sister did. At almost four weeks it was plain that he

could not support himself on his legs. He would roll and pull himself across the room to his mother, resting now and then on his back and waving his paws aimlessly in the air. His mother kept away from him.

As soon as the well kitten, the female, could climb in and out of their low basket, the mother would lie out on the floor of the room and let the well kitten come to be nursed. The male kitten was unable to climb the three-inch barrier. Unless I lifted him out and gave him to his mother she would not nurse him but she washed him carefully and whimpered over him often. He was gay and happy, purred loudly when stroked, and tried to play with his more active sister. If I supported his chest he would try to lap, but unsupported, he took a nose-dive into the saucer. He was so very placid and even-tempered that we thought he might be blind. My son tested him with a flash light and he blinked so normally that we decided that he was able to see but did not react quickly to dangling strings or other playthings.

Up to the time of death the kitten was never able to maintain the optimum physiologic posture. It made attempts to assume this position but in the effort would fall forward on its nose, or to one side. It succeeded in pulling itself along slightly while lying on its side. While in the latter position it was able to use the forelegs, in a well coördinated fashion, to play with articles that were dangled before it or placed on the floor near it. In these playful maneuvers the head and neck movements were well coördinated. The head required support when the animal was given milk, otherwise its nose would forcibly hit the bottom of the dish and then be withdrawn quickly, due to the asynergia of the neck musculature. Lateral movements of the head and neck were executed with but slight evidence of incoördination.

When placed in a tub of water the animal first assumed a position on its back. Its efforts to keep its nose out of the water were not successful and the animal had to be removed to prevent drowning. After an interval of ten minutes the animal was placed in the water a second time and, on this occasion, was much more successful in the efforts to keep its nose out. In doing this vigorous use was made of all of the axial and appendicular musculature and the result was a circus movement.

The pupillary reactions to light were prompt and no spontaneous nystagmus was observed. On douching the ears with hot water, nystagmus was promptly induced with the rapid components towards the side stimulated. With cold water the nystagmus consisted of slower oscillations with less amplitude than was produced by hot water and the differentiation between the rapid and slow components

was much less marked but the movements were slightly more rapid to the side opposite the one stimulated. The patellar and ankle jerks were present on both sides.

The clinical features clearly indicate severe defects of the kinetic mechanisms, both in the static phase concerned with the posture and equilibrium and in the dynamic phase concerned with synergized movement and locomotion.

The examination of the brain disclosed that the cerebellum was reduced in all of its dimensions but more so in the antero-posterior direction than transversely. As a control, the brain of a normal sixty-two day kitten was used. In the normal animal the antero-posterior measurement of the cerebellum was 15 mm. as compared with 8 mm. for the pathologic animal, a difference of nearly two to one. In width the normal cerebellum measured 17.2 mm. and the pathologic one 16 mm. In addition to the cerebellar aplasia there was also an agenetic defect of the right frontal and parietal areas in the vicinity of the sylvian fossa.

After fixation in Muller's fluid for several weeks the brain was imbedded in celloidin and serial sections, fifty micra thick, were cut from the level of the nuclei gracilis and cuneatus to the tips of the frontal lobes, and for this study every fifth section was stained by the Kulschitsky modification of the Weigert-Pal method.

MYELENCEPHALON

The most striking feature was the almost complete absence of the pyramidal tract on the right side. Lissauer's zone, the fibers of the dorsal columns, the spinal fifth, the rubrospinal tracts and the fasciculus longitudinalis posterior, were well stained.

The internal arcuate fibers were well seen but they were less numerous and finer than in the control animal. The external arcuate fibers were but few in number and were distinguished with difficulty. On both sides the ventro-lateral peripheral zone, occupied by the dorsal and ventral spino-cerebellar tracts, was very pale and contained only a small number of myelinated fibers. The right side was slightly paler than the left. The area just lateral to the olives and to the emergent fibers of the twelfth nerve, occupied by the uncrossed fibers of the Deitero-spinal tract, was pale and lacking in the normal amount of definition. It was estimated to be about one-fifth to one-tenth of the normal size for an animal of this age. The longitudinal

bundles in the *formatio reticularis* were paler and more poorly defined than in the control animal. The deficient myelination of the dorsal and ventral spino-cerebellar tracts was of course reflected in the restiform bodies which were pale in the peripheral zones but possessed well stained core bundles.

The myelinated fibers in the gray matter were less numerous, more delicate and smaller than in the control animal. There were many



FIG. 176. Superior surface of the brain and spinal cord showing the defective development of the right cerebral hemisphere and the diminutive cerebellum.

bulbous and bead-like swellings of the myelin. This was especially noticeable in the decussating fibers dorsal to the central canal.

The eighth, ninth, tenth, eleventh and twelfth nerves were all smaller and less densely stained than those of the control animal. The fasciculi were smaller and the fibers more delicate. The cochlear division of the eighth was slightly smaller on the right than on the left side.

The measurements of the inferior olives in their cephalocaudal diameters showed a reduction of about 25 per cent; this measurement was 4 mm. as compared with 4.7 mm. for the normal animal. The lateral diameters of the inferior olives did not show any variation from the normal control and were equal on the two sides. Attention was also given to measurements of the several constituents of the olives and approximately the same ratio obtained for the individual constituents as for the whole structure.

These measurements are shown in table XIII. The terminology of "fish old" for the mesial portion, "bird old" for the dorso-mesial

TABLE XIII

PLANIMETRIC MEASUREMENTS OF THE PRE-CEREBELLAR, AND INTRA-CEREBELLAR NUCLEI, CEREBELLUM AND JUXTA-RESITFORM BUNDLES

	PATHO- LOGICAL	NORMAL
Pre-cerebellar nuclei (longitudinal dimensions):		
Mesial or "fish old" olive.....	4.0	4.7
Dorso-mesial or "bird old" olive.....	3.75	4.0
Chief or "mammal old" olive.....	1.5	2.0
Schwalbe's area.....	3.0	4.5
Deiters' area.....	5.0	5.0
Intra-cerebellar nuclei (longitudinal dimensions):		
Mesial (fastigius and globosus).....	2.5	2.75
Lateral (dentatus and emboliformis).....	3.5	3.5
Cerebellum:		
Longitudinal dimensions.....	8.0	15.0
Transverse dimensions.....	1.6	1.72
Juxta-restiform bundles:		
Longitudinal dimensions.....	1.5	2.75

portion and "mammal old" for the chief or intermediate portion was suggested by Dr. Frederick Tilney in a personal communication concerning some of his as yet unpublished studies on the comparative morphology of this structure. These terms have a connotative significance that justifies their use. It should be noted that the chief or neo-olive, which is the mammalian contribution to the evolution of this structure, is more deficient than either the mesial or the dorso-mesial portion which together constitute the paleo-olive.

The olivary convolutions lacked the sharp outlines seen in the normal animal. The borders were irregular, crenated and lacking in

the rotundity so characteristic of these structures normally. The lack of definition of the inferior olives was due in part at least to the reduction of the size of the core bundles and the circumscribing fasciculi, but in addition to this there was disorder in the arrangement of the cells of the olivary cortex.

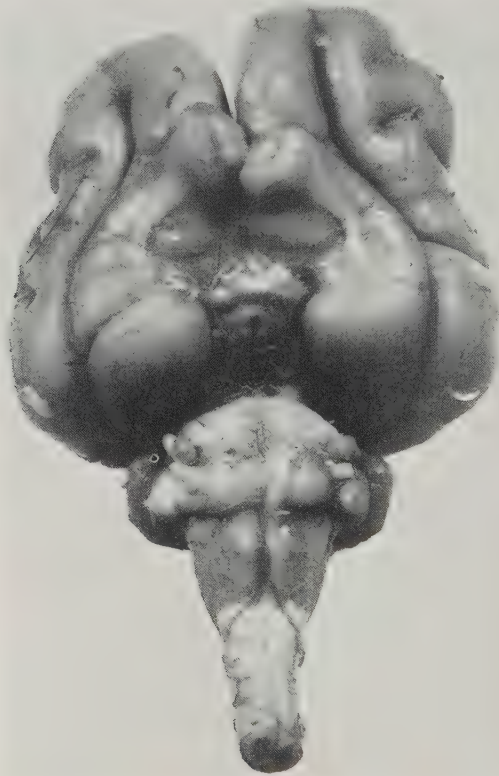


FIG. 177. Inferior surface of the brain and ventral surface of the spinal cord

METENCEPHALON

The juxtarestiform bodies disclosed the most striking pathologic features. The cephalo-caudal measurement was 1.5 mm. as compared with a measurement of 2.75 mm. for the normal animal. The definition of these structures was very poor and the fiber bundles were



FIG. 178. Right lateral surface of the brain and spinal cord showing the morphologic defect in the vicinity of the Sylvian fossa and the diminutive cerebellum.

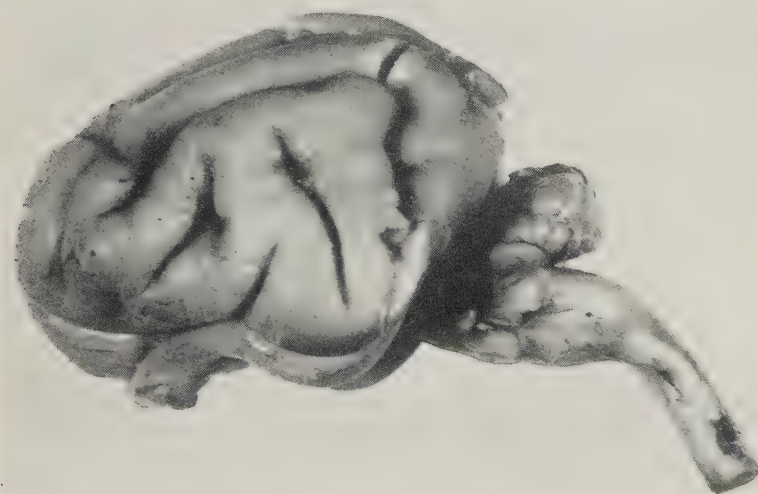


FIG. 179. Left lateral surface of the brain and spinal cord

small in size and greatly reduced in number. The bundles that were present were very pale as compared with deeply stained and dense corresponding structures in the normal animal.

The areas occupied by the nuclei of Deiters and Schwalbe were measured. Deiters' area showed no variation in size from the normal. In both cases the cephalo-caudal diameters were 5 mm. The cerebellar fibers emerging from Deiters' area were, however, very pale and



FIG. 180. Section through the myelencephalon at the caudal extremity of the inferior olive. Note the reduced size of the right pyramid, the small number and delicacy of the internal arcuate fibers, the relative absence of external arcuate fibers, the deficiency of the dorsal and ventral spino-cerebellar tracts, the delicacy of all fiber constituents in the gray matter, and the reduced size and paleness of the longitudinal bundles in the formatio reticularis. Compare with similar level in a normal sixty-two day kitten shown in figure 208.

grouped into small bundles that were fewer in number than in the normal animal. Schwalbe's area measured in its cephalo-caudal extent 3 mm. as compared with 4.5 mm. in the normal (table XIII).

The superior olives were poorly defined and the fibers leading from them were reduced in number and size. The myelinated fibers originating from the medullary centers of the superior olives consisted of a very small number of loosely arranged fasciculi.

The acoustic tubercles were smaller on both sides than in the control animal and appeared slightly smaller on the right than on the left side.

The sixth and seventh nerves showed no variation from the control animal. The mesial and lateral cell masses of the cerebellum did not appear much, if any, reduced in size but the deficiency of the fiber constituents that normally circumscribe these structures left them without definitive outlines. The lateral nuclear mass, com-

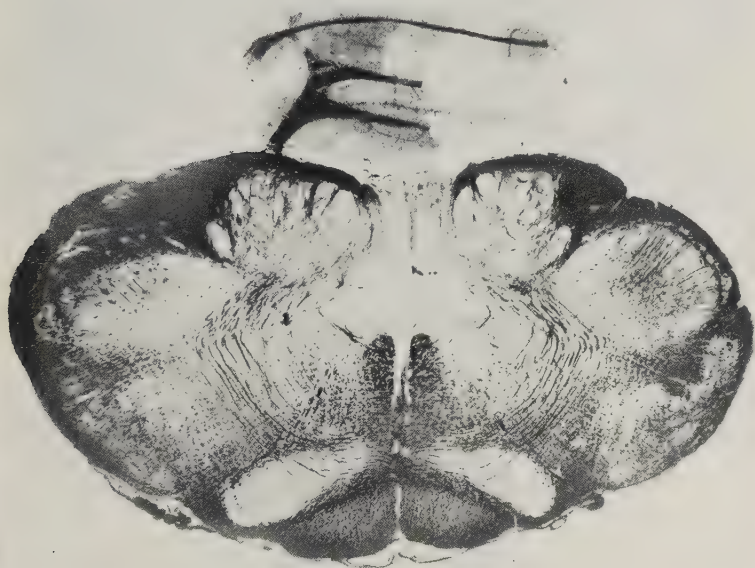


FIG. 181. Section through the myelencephalon of a normal sixty-two-day kitten for comparison with figure 180.

prised of the dentatus and emboliformis, measured 3.5 mm. in its longitudinal (cephalo-caudal) diameter which was the same as the normal animal. The mesial nuclear mass, consisting of the fastigius and globosus, measured 2.5 mm. cephalo-caudally as compared to 2.75 mm. for the normal animal (table XIII). The decussation over the nuclei fastigii consisted of merely three or four bundles of fine fibers. Several large lacunae were present in the lateral nuclear group.

All of the core bundles of the cerebellum were small, poorly stained and comprised of fine delicate fibers. The uvula consisted of three poorly differentiated folia. The paraflocculus presented as a very primitive structure that could not be differentiated from the tonsil. Both crura of the lobulus ansiformis appeared rudimentary and faintly

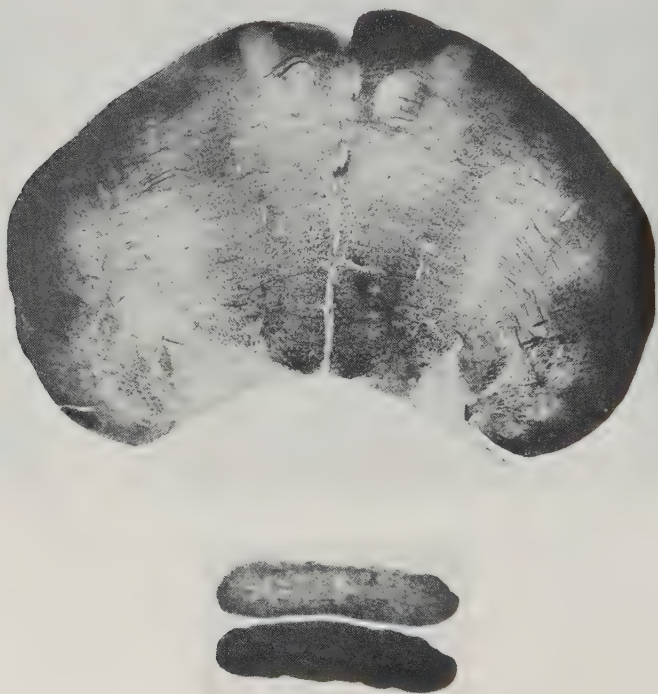


FIG. 182. Section through the myelencephalon at the cephalic extremity of the inferior olives. Note the primitive structure of the caudal extremity of the cerebellum which makes its appearance at this level.

stained. The paramedian lobes were faintly stained, lacking in structural differentiation and consisted of three folia.

The central core of the pyramis was more deeply stained and consisted of denser fibers than any other portion of the cerebellum. The largest fibers of the middle peduncle could be traced to the

vicinity of the pyramis and suprapyramis. All of the lobular and folial patterns of the vermis and lateral lobes were deficient and the



FIG. 183. Section through the spinal cord of a normal sixty-two-day kitten at the caudal extremity of the nuclei of the columns of Goll to show the amount of cerebellum in comparison with that seen at a much higher level in the pathologic animal figure 182.

fiber constituents were meagre. In no location was it possible to distinguish more than a few fibers ascending from the medullary core

to the molecular layer. In consequence of this the longitudinal fibers in the molecular layer consisted merely of a few delicate threads. Anterior to the fissura prima transverse fissures were absent and there was practically no foliation.

Both middle peduncles were reduced in size and on the right the staining was paler than on the left. The superior peduncles showed only a slight reduction in size as compared with the normal control. The dorsal and ventral decussations of the superior peduncles, the thalamo-olivary tracts, the fasciculi longitudinales laterales, the

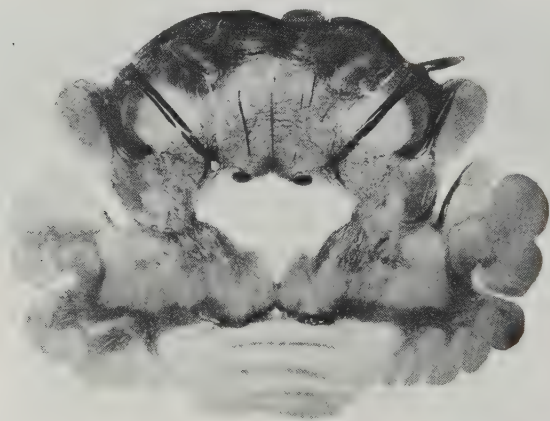


FIG. 184. Section through the metencephalon to show the rudimentary appearance of all of the constituents of the cerebellum, the lack of definition of the intracerebellar nuclei, and the deficiency of the juxtarestiform bundles. Compare with figure 185.

mesial and lateral lemnisci, the mesencephalic fifth and the trochlear decussation compared favorably with similar structures in the normal animal.

MESENCEPHALON

With the myelin stains the superior and inferior colliculi with their brachia, the third and fourth nerves, the red nuclei and the fasciculi retroflexi did not show any appreciable variations from the normal animal. The optic nerves, chiasm and tracts appeared quite normal.

DIENTEPHALON

Technical difficulties precluded a detailed study of the thalamic ganglia at this time and the results of this investigation will be published at a later time if the pathologic morphology warrants it.



FIG. 185. Section through the metencephalon of a normal sixty-two-day kitten for comparison with figure 184.

TELENCEPHALON

The centrum of the right hemisphere was almost entirely devoid of myelinated structures but consisted of numerous corpora amylacea surrounded by a dense mass of cellular material among which fibrillar structures of glial nature could be distinguished. Capillaries were very abundant. The cellular structures consisted of small, round, deeply stained nuclei (microglia), larger round and cuboid nuclei

with less dense chromatin (oligodendroglia) and still larger nuclei resembling in size those of protoplasmic and fibrous glial astrocytes. The ventricle was dilated and the lining ependymal cells were either entirely lacking or arranged in rows of from four to eight cells. The latter picture was more frequently seen. In many localities the ependymal cells were grouped in clusters forming irregular nodular masses. Beneath the ependyma there were isolated groups of densely arranged small, round, deeply staining cells that were disposed parallel to the ventricular wall. At the tips of the ventricles these cellular masses extend out towards the periphery as finger-like prolongations.

In the left cerebral hemisphere the same condition obtained except in lesser degree. The centrum hemiovale contained many corpora-amylacea surrounded by a dense mass of glia cells and fibers and many young capillaries. The ventricle was not dilated as was the case on the right side but the ependyma was heaped up and consisted of several layers of cells with many ependymal granulations. In contrast to the right side there was fairly broad strip of myelinated fibers but this was less than in the normal animal.

In the cortex and subcortex of both hemispheres glia nuclei were more abundant than normally and rod cells were present in all of the laminae.

There was no perivascular infiltration in any portion of the cerebrum, nor was there any cellular exudate into the spaces of the pia-arachnoid. The pia appeared normal but the arachnoid was thickened in some areas. The blood vessels showed no pathologic changes.

No detailed study of the cellular structures was possible because of the preliminary fixation with Muller's fluid and the thickness at which the sections were cut. There appeared to be, however, a superabundance of glia nuclei in the gray matter of the medulla oblongata and the cells of the ventro-mesial and ventro-lateral groups in the upper cervical region and medulla oblongata appeared to be reduced in number and size. Although the number of cells in the nucleus hypoglossus, nucleus ambiguus, nucleus dorsalis of the tenth and the nucleus of the fasciculus solitarius compared favorably with the normal control animal, their size was diminished.

The cells of the inferior olives were small in size and there was complete absence of any orderly arrangement. This same feature was noted in all parts of the cerebellum—the differentiation into molecular, granular and medullary layers being almost entirely lacking. In a few localities scattered groups of granular cells could

be distinguished. They were very small and intermingled with them in a disorderly manner were some Purkinje cells. In the lobus biventer and the central folia of the pyramis the granular layer more nearly resembled the normal appearance than in any other part of the cerebellum, but even in these localities it was thin and consisted of underdeveloped cells intermingled with which were atrophic and misshapen Purkinje cells. Scarcely any cellular elements were distinguishable in the molecular zone of the cerebellum.

DISCUSSION

The clinico-pathologic features here presented are in agreement with the conceptions that the patterns for many of the unlearned reactions are phyletically conditioned and that the formulae for these patterns reside in the phylogenetically older regions of the brain and spinal cord. We know that at birth, or very soon thereafter, all of the spinal and cranial nerve roots of a cat are myelinated.¹ The tracts of the central nervous system that first receive their myelin sheaths are the fasciculus longitudinalis posterior, the fasciculus predorsalis, the vestibulo-Deiterso-spinal complex, the cochlear tracts, the ascending mesencephalic and the descending spinal trigeminal bundles. Later the spino-cerebellar tracts with their connections to the vermis of the cerebellum, the cerebellar peduncles, the rubro-spinal and the optic tracts receive their myelin. The behavioral studies made by Tilney and Casamajor indicate that a distinct correlation exists between somatic behavioral components and myelinogenesis.

The earliest reaction pattern is concerned with posture and balance (vestibulo-Deiterso-spinal). Tilney and Casamajor have enumerated the reactions of the domestic cat in the following order:

- | | |
|-------------------------|-------------------------------------|
| 1. Postural | 10. Scratching |
| 2. Crawling—approach | 11. Avoiding |
| 3. Sucking | 12. Running |
| 4. Synergizing | 13. Pawing |
| 5. Primitive escape | 14. Washing |
| 6. Eye opening | 15. Auditional head and ear turning |
| 7. Eye and head turning | 16. Lapping |
| 8. Sitting | 17. Escape |
| 9. Walking | 18. Climbing |

¹ Tilney, F., and Cassamajor, Myelinogeny as applied to the study of behavior. *Arch. Neurol. & Psychial.*, xii, 1-66, 1924.

At least the first seven of these may be accounted for by the function of pathways consisting of cranial and spinal nerves which by way of the posterior longitudinal and predorsal fasciculi establish connections with the nuclei in the reticular formation of the mid brain, bulb and medulla. An early contribution to synergized movement is supplied by the structures of the paleocerebellum consisting of the vermis nuclei with their connections, the paleoolive, the nucleus ruber, the substantia nigra, the thalamus and the paleostriatum. In the neocerebellum represented by the lateral lobes and the newer structures of the cerebrum represented by the neostriatum and pallium probably reside the pattern formulae for the more complex and finely executed expressions of posture and movement—those late manifestations of somatic behavioral adaptation.

The simplest movement patterns require merely harmonious action of the axial musculature with coördination from segment to segment and bilateral synchrony. Such movements as swimming and the vermicular movements of reptilia and some amphibia (urodeles) require no independence of the extremities but merely bilateral coördination. In consequence of the demand for more perfect unilateral synergic control on the part of the bipedal mammals, and even in some of the lower mammalian quadripeds the cerebellar hemispheres make their appearance. According to Bolk the anterior and posterior crura of the lobulus ansiformis are present in all mammals and contain unpaired centers for coördination of the muscles of each extremity. As we ascend from the lower to the higher mammals and as the independent movements of the limbs become more complex the cerebellar hemispheres acquire more complexity in their lobular and folial patterns—thereby providing the neural centers and pathways necessary to unilateral synergic control of the individual movements of the extremities. This greater range of movement therefore is accompanied *pari passu* by the development of greater cerebellar area.

In this case a part of both the neo and paleo structures was deficient as a result of arrested development. This arrest affected principally the right cerebral hemisphere, more especially the frontal and parietal areas with their pontile connections, but the same process affected, to a lesser degree, the medullary substance of the left cerebral hemisphere. The cerebellum, however, suffered the most and none of its constituents escaped. Every lobe, lobule, folium and foliette, to-

gether with their finer components, showed the results of arrested development.

SUMMARY

The total myelinization in all of the afferent and efferent cerebellar tracts was less than it should have been in a normal animal of this age. The main functional defect in this kitten was the inability to assume or maintain the optimum physiologic posture, that is, the position of lying on its belly so that it could bring both legs under it. The animal could not get into this position and in attempting to do so would roll over.

The animal was born without and never developed those tracts essential to the assumption and maintenance of the optimum posture. Throughout life the chief symptoms were due to this very defect. This posture assuming function is the first component of behavior to make its appearance in the new born kitten. It appears on an average of eight minutes after birth. At this time both the juxtarestiform bundles and the vestibulo-Deiterso-spinal tracts are well myelinated.

This animal showed but few signs of asynergia in the head and trunk movements and none in the limb movements, but it must be remembered that all of these movements were still of the most simple and primitive type. The cerebellum, although only slightly in excess of 50 per cent of the normal size for this age, developed sufficient synergic capacity to give the animal adequate coördinative control in such movements as it did make. Because of its inability to assume the correct posture, it was unable to learn such acquired performances as washing its face with its paws, standing, walking, running, climbing, jumping, burying its feces, hunting or any other skilled acquired acts.

The agenetic defect of the right frontal and parietal areas, the bilateral lesions in the centrum ovale and the diminutive pyramid on one side, are other indications of the widespread morbid process in the brain that was operative in the prenatal period. That the animal showed no evidence of pyramidal disease as indicated by paralysis, lack of voluntary control, increased reflexes and tone, is due to the fact that the motor areas of the cortex are not essential for the early behavioral reactions in the kitten, and that a large range of movements such as crawling, swimming and pawing, all with a more or less definite purpose, are possible through the activity of lower segments in the axis, probably the mid-brain. The absence of the pallio-ponto-

cerebellar connections from the right hemisphere and the deficiency on the left side, is a histological condition which did not express itself in the symptomatology, because the animal had not advanced to that stage of motor organization in which neopallial-cerebellar coöperation is essential. This coöperation is necessary only to more highly skilled learned reactions.

CHAPTER XVI

ORIGIN OF THE CORTICO-CEREBELLAR SYSTEM AS DETERMINED IN HUMAN PATHOLOGICAL MATERIAL¹

N. W. WINKELMAN, M.D., AND JOHN L. ECKEL, M.D.

CASES with focal cortical lesions are comparatively rare in human autopsy material. The time of death in cases with limited pallial involvement is variable and does not always take place within the three months necessary for Marchi staining. Human material, is thus necessarily limited in the number of available cases. However, using material obtained over a period of about five years, we have been fortunate enough to get cases with lesions of nearly every part of the cerebral cortex.

ANATOMY

Certain facts are definite and well established anatomically, *i.e.*, that the cerebellum is connected with the opposite cerebral cortex through the cortico-ponto-cerebellar system. The course of this system through the internal capsule, cerebral peduncle and pons is beyond question, but the exact sites of origin of these fibers is still in dispute. Some investigators go so far as to say that every cortical area contributes fibers to this system. Others limit not only the number of cortical areas but even the exact parts of the major cortical fields. It is also established that it is impossible to trace degeneration beyond the pons from a cortical lesion involving the cortico-ponto-cerebellar system.

THE FRONTAL LOBE

Most investigators are agreed that the frontal lobe takes part in the formation of the cortico-ponto-cerebellar system, that these fibers course through the corona radiata into the anterior limb of the internal capsule and descend in the inner fifth of the peduncle and arborize

¹ From the Wards and Laboratory of Neuropathology of the Philadelphia General Hospital.

about cells in the nuclei of the basis pontis. The exact site of origin of these frontal fibers is still in controversy. Edinger (1) quotes Quensel in stating that the frontal fibers arise from the posterior portion of the first frontal convolution on the external surface and the median surface of the frontal area anterior to the knee of the corpus callosum. Déjerine (2), shows by careful study that lesions of the anterior half of the frontal lobe produce secondary degenerations in the corona radiata, anterior limb of the internal capsule, the pulvinar of the thalamus and the anterior portion of the red nucleus, but that the fibers cannot be traced into the foot of the peduncles. It is probable that this is the tract that is involved in the experimental work on the frontal lobes in lower animals in the production of decerebrate rigidity. In the case (Cas Heudebert, p. 140, tome 2) studied by Déjerine, with a lesion of the middle third of the motor area and the adjacent posterior part of the frontal lobe, he found degeneration of the inner two-fifths of the cerebral peduncle. Flechsig (3) likewise feels the tract comes from the posterior portions of the frontal convolutions. Von Monakow (4) believes that it takes origin from F-1 and F-2 and the frontal operculum. He reports a case of frontal lobe hemorrhage in which there was found degeneration of the fronto-pontile fibers extending to the pontile nuclei with some fibers terminating in the internal geniculate body. In another experiment von Monakow removed the right half of the pallium of a dog and at death some time later he found atrophy of the right cerebral peduncle, including the inner fifth and the pyramidal tract, both of which extended into the pons. There was also degeneration of the pontile nuclei, with atrophy of the homolateral pulvinar of the thalamus and some of the cells of the red nucleus, and a shrinkage of the opposite or left middle cerebellar peduncle, thus showing a definite crossed cerebro-cerebellar connection.

Mingazzini (5) repeated the work of von Monakow and obtained similar findings. Turner (6) and Meynert (7) were the first to show these crossed cerebro-cerebellar connections but the anatomical relations and details were worked out later by others.

TEMPORAL LOBE

It is definitely established that there is a tract from the temporal lobe of the pontile nuclei. While the exact site of origin of this tract is still not absolutely defined, its course is well known. From the

posterior portions of the lower temporal gyri (its most probable place of origin) the fibers pass below the putamen and join the posterior portion of the internal capsule in the sublenticular region, thence to the outer fifth of the cerebral peduncle into the ventral portion of the pons. Von Monakow states that while most of these fibers end in the pons a few proceed to the internal geniculate and posterior quadrigemi-

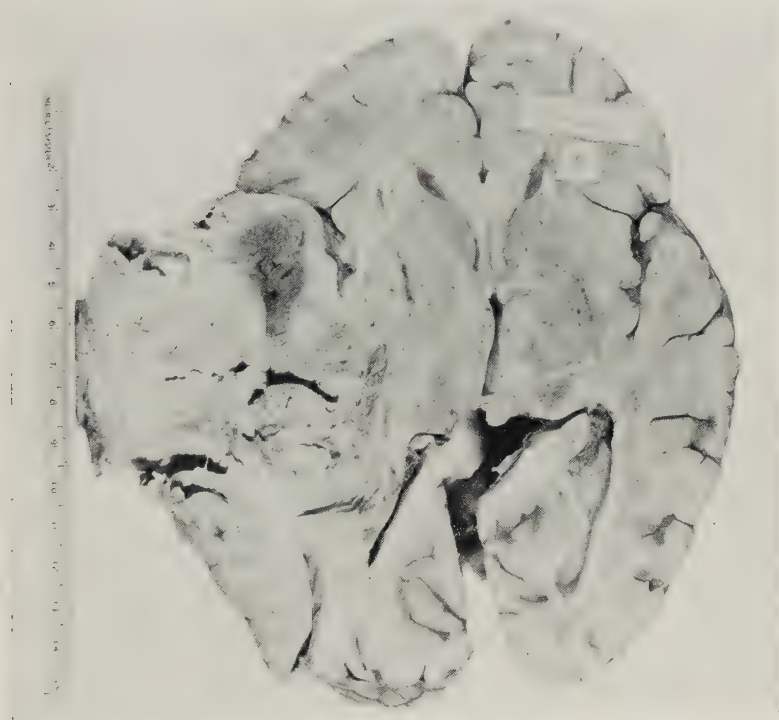


FIG. 186

nal bodies. This tract, first described by Türck (8) in 1851, was carefully investigated by Déjerine and Kam (9). Since their contributions a number of investigators have also corroborated the existence of this tract. Early it was considered sensory by Meynert because it did not degenerate downward after a lesion of the internal capsule in its *usual location*. Subsequent work, however, has shown that it does degenerate downward to the pons.

While the pallial area of this tract is not absolutely fixed, apparently the posterior portion of the second and third temporal convolutions



FIG. 187

must be involved before degeneration occurs. Déjerine, Kam, Marie and Guillain (10), Rhein (11) and others have demonstrated this. Ferris and Turner (12) have found this tract in monkeys, while Beevor

and Horsley (13) also found these fibers coming from the temporal area in their experimental work on cats. Edinger is of the belief that this tract arises from the second and third temporal convolutions and from a not yet sharply defined area of the lateral occipital lobe. Marie and Guillain in a series of nineteen cases found the most usual position for the lesion to be the posterior segment of the internal capsule, and in the white matter situated between the temporal convolutions and the external wall of the occipital horn of the lateral ventricle. They state it is through this area that fibers from the third temporal convolution pass on their way to the internal capsule.

OCCIPITAL LOBE

Whether the occipital lobe contributes fibers to the cortico-ponto-cerebellar system is still uncertain. The only case we could find in the literature was that published by Dr. Adolph Meyer (14), 1907, wherein a bullet wound destroyed portions of the parietal and occipital lobes. In this case Dr. Meyer was able to trace degeneration by the Marchi method into Türck's bundle. One gets the impression in reading this report that the temporal lobe fibers may have been caught in the path of the bullet wound. Déjerine, in his book, states that occipital lobe fibers do not enter into the formation of the peduncle and that the occipital lobes do not send projection fibers into the cortico-pontile system. In no case did Déjerine trace fibers from the occipital lobe into the peduncle.

PARIETAL LOBE

From the parietal lobe we have been unable to find a definite statement backed by pathological or experimental proof wherein the author was positive that he had found fibers arising from this lobe and terminating in the pons. Most all investigators who have worked upon this problem believe that such a tract from the parietal lobe exists, but that definite proof is still wanting. Déjerine is one of the few who states plainly that the parietal lobe, especially its posterior portion, does not give fibers to the cortico-pontile system, but makes connection with the thalamus and red nucleus.

MOTOR CORTEX

From the cerebrospinal system numerous collaterals have been demonstrated terminating in the pontile nuclei.

CASE HISTORIES

Case 26-291, a white male, aged 58. For two years dullness, irritability and mild headache, which gradually became severe, particularly the two weeks preceding death. Several days before death he passed into coma from which he did not arouse. Necropsy revealed a large cystic glioma involving most of the left lower frontal lobe, extending backward into the temporal lobe. The cyst was 6 cm. in diameter. Multiple small pontile hemorrhages were found. No degeneration was present on the inner or outer sides of the peduncle.

Case 23-290, a male, aged 79, a laborer. Right sided "stroke" eight years previously; another ten days before death. Examination showed pyramidal tract signs on the right, including Babinski. No evidence of any cerebellar disease. At postmortem the brain revealed a large area of softening, involving the left lower motor zone, including Broca's area and the inferior frontal convolution to within 5 cm. of its tip. There was a recent area involving the inferior frontal convolution on the right. Sections of the peduncle failed to reveal any degenerative changes.

Case 26-268, a colored man, aged 35. He was taken ill with an attack of acute meningeal symptoms, with death in two weeks. Postmortem revealed meningeal involvement with a large area of hemorrhage involving the inferior orbital areas and left frontal area. Examination of the peduncles in this case failed to reveal any areas of degeneration.

Case 27-32, a white male, aged 66. Three weeks before admission he suddenly became confused. He was poorly oriented and had difficulty in speaking. There was no weakness of any of the limbs. In a few days aphasia became complete. He failed rapidly and died twenty-two days from the onset. Necropsy revealed sclerosis of the basilar vessels. There was a small area of softening in the left tegmentum of the pons and a more extensive softening in the left cerebral hemisphere, corresponding to the supply of the Sylvian artery. It particularly involved Broca's area. There were no degenerated fibers traceable into the inner side of the peduncle. The left pyramidal tract, however, showed a moderate amount of degeneration.

Case 27-175, a white male, aged 68. There was a primary carcinoma of the prostate with metastasis into the region of the femur, necessitating amputation. For ten months he had been constipated and had marked pains in the rectum. Upon admission he presented neither mental nor neurological signs. Within a few weeks, however, he began to show confusion, general weakness, dullness and complained of headache, which increased and he died within eight weeks from the time he entered the hospital.

Necropsy revealed an area of softening of the left cerebral hemisphere, limited to the lower parietal and the posterior parts of the temporal convolutions. Grossly it was egg-shaped, with the greatest involvement in the deeper parts of the temporal lobe. There was marked degeneration of Türck's bundle by Marchi stain.

Case 26-338, a female. Onset about December, 1925, with frontal headache, which soon became constant. In February, 1926, nausea and vomiting developed. Some time later failing vision began, which gradually progressed. Then she found difficulty in getting the proper words. Physical examination revealed par-

tial aphasia with active reflexes on the right, with an occasional Babinski reflex present. No definite cerebellar symptoms present. Her strength gradually failed and she died.

At necropsy a tumor 6.5 cm. in diameter, involving the left temporal lobe, particularly the anterior portion of the first and second convolutions was found. The claustrum and the external capsule were involved, also the island of Reil, and it pushed the basal ganglia considerably inward (fig. 186). The internal capsule was not directly involved. In the midbrain a marked degeneration of the left pyramidal tract was present. The outer fifth of the peduncle, which contains the fibers of Türck's bundle, showed a mild degree of degeneration.

Case 23-204. A 60-year old man with sudden onset of right hemiplegia and aphasia. Death occurred within six weeks. Autopsy showed a left temporal lobe softening, involving largely the first and second temporal convolutions, also the Island of Reil, the lenticula and part of the posterior internal capsule. Sections of the brain stem stained by Marchi method, gave degeneration of a mild degree in the left pyramidal tract. No degeneration of the external or internal fifths of the peduncle. The substantia nigra was intact.

Case 27-25, a white female, aged 50. Left hemiplegia occurred August 27, 1926, following which considerable improvement occurred. October 17, 1926, a second attack on the same side occurred, which again slowly improved. January 14, 1927, a general convulsion, in which she died. Autopsy revealed a large area of softening in the right hemisphere, limited to the area of supply of the Sylvian artery. Examination of the peduncles failed to reveal degeneration on either side.

Case 27-115, a white male, aged 42. The duration of the last illness was seven weeks. This began with chills and fever, associated with severe bronchitis, from which he did not improve but gradually lost weight and strength and died. It was noted that there were present residuals of an old left hemiplegia. At autopsy the brain weighed 1360 grams. The right cerebral hemisphere showed many areas of softening, scattered through the various lobes. The size of the right hemisphere was approximately three-fourths that of the left. There were a number of areas showing loss of cortical substance, varying from 1 cm. or more in diameter and 2 cm. in depth. One of these was in the superior or first frontal convolution, another in the parietal lobe at its junction with the Sylvian fissure, and another in the occipital lobe, measuring 4 cm. in length, 2.5 cm. in breadth and about 0.5 cm. in depth. The basilar vessels were very much thickened and showed plaques. Careful staining of many sections failed to show any degeneration in either Arnold's or Türck's bundle. There was moderate degeneration of the right pyramidal tract.

Case 24-75, a white male, aged 75. This man was picked up unconscious on the street and brought to the hospital. Upon admission there was projectile vomiting, conjugate deviation of the eyes to the right; no definite weakness of any of the limbs could be made out. He did not regain consciousness and died on the ninth day. Autopsy revealed a large hemorrhage in the right parieto-occipital area with no degeneration appearing in the peduncles in any tract (fig. 187).

Case 26-252, a white male, aged 67. Left hemiplegia occurred ten days before admission. At the hospital he showed considerable mental deterioration. There

was weakness of the left side with marked diminution of tactile sensation. There were increased tendon jerks on the left side and a positive Babinski. He died in the tenth week. Postmortem revealed softening in the right hemisphere in the area supplied by the Sylvian artery. This area extended backwards into the occipital lobe. In the left hemisphere there was recent area of thrombotic softening, limited to the parieto-occipital lobe. The temporal lobes were not involved in either hemisphere. No degeneration was shown in the outer fifth of either peduncle.

Case 26-317. This case presented sudden onset of weakness of right side of the body with difficulty in using the tongue. He presented all of the indications of increased intra-cranial pressure, associated with right sided weakness, with clonus and Babinski sign.

Autopsy revealed tumor in the left parieto-occipital region, which proved to be an infiltrating glioma. Sections of the peduncles failed to reveal any degeneration.

Case 26-259, a white female, aged 61. She had had a right hemiplegia two years prior to admission. During the past year she was forgetful and childish and there was gradual failure and death. Postmortem revealed a softened area of the right occipital lobe. Another of the left temporo-occipital lobe, including the visual area. This was of thrombotic origin. In the left lenticulo-capsular region there was a third area of softening. It will thus be seen there was bilateral occipital lobe softening. No degeneration of fibers could be traced into the outer fifth of either peduncle in Marchi and Weigert preparations.

Case 26-296, a white male, aged 69. He had an attack with right hemiplegia one month before admission to the hospital, associated with motor aphasia. He lived for a period of six months. A general convulsion preceded death. Necropsy revealed a softened area located in the left motor and parietal area, which was more or less limited to the supply of the Sylvian artery. No degeneration of Türck's bundle was demonstrated by the Marchi or Weigert stain.

DISCUSSION AND CONCLUSION

The determination of the cortical areas from which fibers arise to enter the formation of the so-called pallio-ponto-cerebellar system is of more than theoretical interest. That it occurs in its most highly developed state in man and that it does not occur in the lower vertebrates, and that it is more massive than the cortico-spinal system leads to the conclusion that it is an important connecting link between the cerebrum and cerebellum. The course of these fibers is established; the exact origin for most of the fibers is still a matter of controversy. How important it is to determine the points of cortical origin can be easily seen when one considers the fact that certain cerebral lesions may show clinically cerebellar signs in the absence of pressure symptoms. If cerebellar signs are present in cerebral lesions and the exact points of origin of the cerebellar system of fibers are

determined, it would give us additional evidence for more accurate cortical localization.

Much has been written regarding the differential diagnosis between frontal lobe and cerebellar lesions, especially tumors. It is quite possible that involvement of the cortico-cerebellar system in frontal lobe lesions is an explanation for the symptoms that may result. If we are able to establish a more accurate origin for these fibers, surgical procedures might be carried out earlier and to greater advantage. It is almost universally agreed and our own cases bear this out, that the anterior half of the frontal lobe does not take part in the formation of the frontal portion of the cortico-cerebellar system, or what is known as "Arnold's bundle." In suspected lesions, therefore, of the frontal area, the absence of cerebellar signs might be of value in limiting the lesion to the anterior half of the frontal lobe, and the presence of cerebellar signs to the posterior portion. Anything which will increase our diagnostic ability as regards the frontal lobe is to be welcomed. Expansile lesions by pressure may, of course, give neighborhood symptoms, and these must be carefully evaluated. In our cases we found none in which degeneration of Arnold's bundle could be established. In an analysis of these cases it is found that in all the involvement was within the anterior half, or only in the posterior portion of the lower frontal. None of these areas have been previously shown to give origin to Arnold's bundle.

As far as the temporal lobe is concerned, our facts are somewhat more definite as regards the cerebellar connections. The posterior half of the temporal lobe, especially the second and third convolutions, have been definitely shown to give origin to the temporo-ponto-cerebellar system of fibers, or what is known as "Türck's bundle." One would, therefore, not be surprised to get clinically cerebellar manifestations in lesions in this part of the brain, bearing in mind the fact that cerebellar manifestations are difficult to elicit with our present methods of examination until far advanced. This is fully confirmed by the finding at autopsy of small, unsuspected lesions in the cerebellum itself.

In our material we found definite implication of Türck's bundle in two cases and in both there was disease of the posterior half of the lower temporal convolutions. In lesions of the anterior half of the temporal lobe no such degeneration in Türck's bundle occurred. This has been shown by Mills and Spiller, (18), Déjerine, and others.

It may be well worth recalling that lesions of the internal capsule in their usual location do not involve this bundle because of its low situation in the sublenticular region. Its location in the outer fifth of the peduncular foot is well known.

From the parietal lobe no fibers have yet been demonstrated going into the formation of the pallio-cerebellar system. While it is true that at times in parietal lobe lesions cerebellar signs may appear to be present, due recognition of the part played by the fibers of deep sensibility has to be taken into consideration.

While we were able to find in the literature the report of but one case, that of Dr. Adolf Meyer, wherein there have been fibers traced from the occipital lobe to the pons, it must be said in all fairness that this patient had an extensive gunshot wound of the brain, and the posterior temporal fibers may have been implicated. Flechsig in the description of his occipito-mesencephalic bundle, suggests rather strongly that some of these fibers may arborize in the pons and form a part of the pallio-cerebellar system.

In a clinical evaluation of the symptoms resulting from motor cortex lesions, one must remember that in complete lesions the paralysis which results overshadows all else and does not permit of testing of other motor functions. In incomplete lesions weakness must not be confused with incoordination.

The increased complexity and size of the pallio-cerebellar system in the human as compared to the lower animals forces one to the conclusion of its increased functional importance. The pons is to be considered as the center in which all these tracts converge. To it also the collaterals from the pyramidal tract, the lemniscus and other undetermined tracts higher up (Cajal) come in and are relayed to the opposite cerebellar hemisphere, thus making the pons a very complex ganglion.

SUMMARY

1. A series of fourteen cases with lesions in various areas of the cortex are detailed. In only two was there implication of the pallio-cerebellar system. In both of these Türck's bundle was involved from ablation of the posterior lower temporal convolutions.

2. No fibers from the anterior frontal areas, from the lower frontal or orbital convolutions, from the parietal or occipital convolutions,

could be demonstrated to enter the peduncle and terminate in the pons.

3. Our results agree in the main with those found in the literature.

DISCUSSION

The following questions submitted to Dr. Eckel before the Commission, together with the answers to them, are here reported verbatim.

DR. LEWELLYS F. BARKER: I would like to ask Dr. Eckel if the cases that are recorded, or his own experience, throw any light upon the possibility of return, from the cerebellum to the pallidum, of the impulses that are initiated in the pallidum and pass to the cerebellum? I refer to the return through the superior peduncle.

DR. JOHN L. ECKEL: I did not take up that phase of the work.

DR. ADOLF MEYER: I should like to ask Dr. Eckel and Dr. Winkelman whether they have paid any attention to the condition of the cerebellum in these cases? In infantile lesions and also in lesions of the adult one sees very definite alterations in the opposite half of the cerebellum, which I believe ought to be thoroughly utilized in a study of this kind.

DR. ECKEL: Yes, we have. We did not have any very suitable material for that work, but we are looking for it. There are definite changes which take place in the opposite cerebellar hemisphere, particularly in the infantile cases, but we did not have any good examples at our disposal.

DR. M. ALLEN STARR: Mr. Chairman, when there is a question of pathology, I think we all defer to Dr. Spiller. I would like to know if perhaps Dr. Spiller's observation might throw some light upon this situation.

DR. WILLIAM G. SPILLER: The statement has been made that all parts of the cerebrum are connected with the cerebellum. I am not aware that this statement rests upon satisfactory anatomical study. The work of Déjerine has been of special value in determining the connections of the cerebrum with the cerebellum. His method of investigation has depended on serial sections of lesions of a destructive character and not on degenerations caused by tumors. The latter are more or less unreliable, because it is difficult to determine the exact limits of tissue affected by a tumor, and because axis cylinders may pass through certain tumors, notably gliomata, without being destroyed.

The researches of Déjerine caused him to conclude that the anterior three fourths of the frontal lobe and the whole occipital lobe, including the angular gyrus, send no projection fibers into the foot of the cerebral peduncle. The internal fifth of the foot of the peduncle is not formed by fibers connected with the prefrontal region, but by fibers arising in the rolandic operculum and the adjacent part of the frontal

operculum, i.e. from the facio-pharyngo-laryngeal motor zone. This view is very different from that held by many, Meynert, Flechsig, and others, *viz.* that the inner bundle of the foot of the cerebral peduncle arises in the frontal lobe.

The external bundle of the foot of the peduncle, the fasciculus of Türck, contains fibers from the middle portion of the temporal lobe, especially from the second and third temporal convolutions. Other investigators have believed this tract had a connection with the occipital lobe. I know of no investigations which have proved that Déjerine's findings are inaccurate. I am unable to cite any findings which prove a definite connection between the parietal or occipital lobe and the cerebellum.

DR. SMITH E. JELLIFFE: I think it is well known to all of us that as far back as 1892 Bruns first called attention to the characteristic cerebellar gait in lesions of the first and second frontal gyri, and since Bruns' first investigation, a number of confirmatory observations have been recorded. Then tonus changes were found in similar clinical involvements, and recently the problem of apraxia has been brought into the foreground as relating to lesions in the first and second frontal convolutions, possibly involving the fronto-ponto-cerebellar pathway.

The problem that interests me particularly, and concerning which I might ask some light, is whether the characteristic cerebellar gait of the frontal cases, the characteristic hypertonicity and hypotonicity and characteristic apraxias are separable from the more distinctly essential cerebellar symptomatology?

DR. JOHN L. ECKEL: I do not think they can be definitely separated, unless one does so in a specific case. We have not had any material of that kind, so that we have not had the opportunity of seeing the clinical record beforehand and the pathological material afterward.

DR. J. RAMSAY HUNT: Mr. Chairman, I would like to ask Dr. Eckel if he has encountered symptoms of tonic perseveration or other tonic phenomena in connection with cases of frontal lobe symptomatology? Kinnier Wilson has observed tonic perseverations in frontal lobe lesions and refers it to the fronto-ponto-cerebellar system.

DR. JOHN L. ECKEL: I have seen it described clinically but I have not had any opportunity to see it proven pathologically.

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Section IV

CLINICAL STUDIES

CHAPTER XVII

CEREBELLAR LOCALIZATION AND SYMPTOMATOLOGY¹

THEODORE H. WEISENBURG, M.D.

PERHAPS there is no subject in neurology today about which there is more controversy than the function of the cerebellum. To a less extent this also applies to the interpretation of symptoms arising from lesions of this organ. In the last decade many excellent papers have appeared on the various aspects of this subject, and while they have enriched our knowledge, they have by no means clarified the problem.

What is the reason for this? The fault in part lies in the nomenclature used in describing the motor disturbances present in cerebellar disease. Some of these are atonia, hypotonia, ataxia, incoordination, dysequilibrium, discontinuity, asthenia, astasia, dysmetria, hypermetria, asynergia, anisosthenia, adynamia, and others which have not been mentioned. It is rarely that two authors employ any of these terms in the same way, or attach to them the same meaning. For example, in a recent article, in the description given of the finger to nose test, the statement read that the patient's movements were asynergic, dyssynergic, hypermetric and ataxic. Atonia and hypotonia are used to describe different symptoms, but usually the same thing is meant. At times terms are so jumbled up that the reader hardly knows what the author means to imply, leaving him with the well grounded suspicion that possibly the writer of the article does not himself know.

Perhaps the chief reason for the discrepancies in description is the fact that *cerebellar disturbances are in motion*. The reeling gait or the incoördinate movement of a leg or arm, because of their very nature, are not easy to describe and analyze. Because of this over

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twenty years ago I began to study cerebellar movements by means of moving pictures. Obviously such a study has great advantages for the camera is quicker than the eye, and what is merely a general impression, which is what most clinical observations are, is capable of careful analysis.

The assumption that the results of experimental lesions in lower animals are always in accord with human symptomatology has contributed to the confusion of the subject, for there is no more accord in the experimental results than in the clinical symptomatology.

The purpose of this paper is to discuss mainly two phases of the problem (1) localization of function, and (2) symptomatology depending upon such localization. It is my contention that such localization exists, and if this were generally accepted the clinical recognition of cerebellar lesions would be made easier.

THE FUNCTION OF THE CEREBELLUM

The phylogeny, comparative anatomy, structural connections and the histology all point to the fact that the cerebellum is a distinctive organ with a uniform structure with a very definite purpose, and that this purpose is to coördinate or synergize all muscular movements. While this is generally admitted there has developed a fundamental difference in its interpretation: (1) those who believe that the entire organ acts in unison or as a whole, and (2) those who believe that the cerebellum has a functional localization. There are authors who attempt to take a middle ground admitting that there may be a prevalence of representation of muscle territories in certain large anatomical divisions of the cerebellar lobes. The first viewpoint is largely held by Luciani and Sherrington, who believe that the cerebellum acts as a single function unit, admitting however functional supervision over the body musculature on each side of the cerebellum.

It is because of this difference of opinion that much of the difficulty has arisen in the interpretation of cerebellar symptomatology. I believe that there is a very definite localization of function in the cerebellum. If there is not then the cerebellum differs from every other part of the nervous system. Perhaps much of the confusion has arisen in what is meant by centers. The cerebellum does not act alone any more than any other part of the brain acts alone. The cerebellum exerts its influence at the same time and in conjunction with the other motor levels, in the motor cortex and the corpus

striatum—through the lowest motor level in the spinal cord. Whenever the cerebellum is thrown out of function whatever activity remains is because of the unopposed action of the remaining physiological levels.

It is not within the scope of this paper to present in full the many evidences which support cerebellar localization. The admitted theories will be briefly mentioned and disputed or new viewpoints elaborated.

The phylogeny and comparative anatomy

It is only necessary to mention that from the phylogenetic viewpoint the cerebellum develops according to the needs of the animal for coördinate function. The comparative anatomical viewpoint is well summed up by Herrick (1) as follows: The afferent system of fibers is distributed within the cerebellar cortex in an arrangement roughly concentric, and the cerebellar cortex accordingly shows an ill defined functional localization determined by the distribution within it, ill-defined because there is considerable overlap of the cortical fields reached by the fiber system. He however states that the afferent fibers terminate according to their development, the vestibular fibers going to the marginal parts, the mesencephalic and spinal systems more dorsally, and the neopallial system reaching the upper surface farther dorsal than the last. He concludes that in the efferent side of the cerebellum of mammals there is an obscure functional localization which like the afferent may be defined in terms of the anatomic connections of the related fiber tracts.

The fiber connections of the cerebellum

When considering the question of localization of function in the cerebellar cortex the fiber connections of the cerebellum must be taken into consideration for their course, connections and terminations point to certain physiological conclusions. Our knowledge of these tracts is being constantly enriched by comparative anatomical studies and by such experimental work as is reported in this meeting by Mussen, Sachs and others, and it is altogether probable that in the course of the next few years many contributions will be added which will show that the cerebellum has many afferent and efferent connections with the spinal cord, medulla, mid-brain and cerebrum, which so far have not been demonstrated.

It is held by some authors (Tilney and Riley (2)) that the cerebellar cortex receives fibers from all parts of the cerebral cortex,² pons, medulla, and spinal cord. These fibers have very definite terminations in the cerebellar cortex. They do not end anywhere. Roughly speaking most of the fibers transmitted by the inferior cerebellar peduncle go to the vermis, although most of the olivary fibers go to the hemispheres, while those coming from the cerebrum through the middle cerebellar peduncles go to the lateral hemispheres. Through these connections the cerebellum is in contact with all types of receptors; by means of the middle cerebellar peduncles with motor and vestibular impulses from the frontal and temporal lobes and possibly sensory and visual impulses from the parietal and occipital lobes; by the inferior peduncle with vestibular impulses relayed from the semi-circular canals, muscle, joint and tendon sensation by means of the ventral and dorsal spinal cerebellar tracts, these impulses being already coördinated and of cerebellar character, and sensory impulses mediating chiefly muscle sense and probably touch sensation by the fibers which come from nucleus cuneatus and gracilis. The function of the olivary cerebellar fibers is not definitely known. They may relay sensory impulses.

There is an extensive bulbo-cerebellar connection between the olivary bodies, the various lateral tract and arciform nuclei, the ocular nuclei and the fifth, seventh, ninth, and tenth cranial nerve nuclei.³ Exact knowledge of these tracts and of their function is still lacking, but the evidence points that these fibers transmit impulses which inform the cerebellum of the condition of the synergic muscles concerned with talking, eating, swallowing and movements of the head and eyes.

We have no definite knowledge of the method of termination of the afferent fibers in the cerebellar cortex. The impulses, however, are integrated by the various cortical cells in a manner which has not been determined, and are then transmitted into the nucleus dentatus, emboliformis, globosus and fastigii. There is a very definite order

² There is some doubt that fibers from the parietal and occipital lobes connect with the cerebellum. André Thomas (3) states that the only cerebral connections are with the Rolandic area, the frontal lobe in its orbital position and the middle part of the second and third temporal convolutions.

³ The reader is referred to the excellent paper by Brun (4) which gives a summary of our present knowledge regarding the fiber connections of the cerebellum.

of termination. They do not end blindly as indicated by Brun. The fibers from the lateral hemispheres or the neocerebellum go into the dentate nuclei almost altogether. The fibers from the paleocerebellum or the vermis and flocculi go into the nucleus fastigii, globosus, emboliformis and somewhat into the dorsal frontal part of the nucleus dentatus. Here the efferent impulses are again integrated and transmitted to the other parts of the nervous system. Most of these go by means of the superior cerebellar peduncle to the nucleus ruber and from there to the spinal cord by means of the rubro spinal tract. These impulses come largely from the nucleus dentatus, but fibers have also been traced from the nucleus globosus, emboliformis and fastigii. The superior cerebellar peduncle also transmits fibers which connect the cerebellum with the opposite cerebrum. These fibers have been traced as far as the optic thalamus.

Efferent impulses are also transmitted into the medulla. They come largely from the paleocerebellum. According to the experiments of Mussen (5) whenever the nucleus fastigii and globosus were injured it was possible to trace two distinct tracts, the hook bundle and the fastigio-Deiters, which ran into the medulla. The hook bundle after decussating, hooks over the superior cerebellar arm and turns ventrally dividing into a median and ventro-lateral portion. The median fibers pass to Deiter's, Bechterew's, nucleus triangularis, then to the sixth nucleus and the posterior longitudinal bundle and the tecto spinal tract. The ventro-lateral portion sends fibers to the motor fifth and seventh and some degeneration was traced to the cortico spinal tract. The fastigio-Deiters terminates chiefly in the Deiter's nucleus of the same side. Cerebello-bulbar fibers have also been observed as ending in the formation reticularis of the medulla where they come in contact with the cells of the dorsal motor nuclei in the medulla. It is reasonable to conclude that through these connections the cerebellum controls the synergic movements of the eyes, talking, eating, swallowing and other bilaterally acting movements.

New rubro spinal connections are described by Mussen. He destroyed first one posterior pole of one red nucleus and then of both. When this was done there was complete bilateral symmetrical degeneration of the rubro spinal tracts, but when he destroyed the anterior pole, *i.e.*, the nucleus parvocellularis of the red nucleus, he found a new tract which crossed immediately and ran laterally to the rubro

spinal field ending in the lower segments of the cervical cord. He called this the rubro cervical tract as distinguished from the rubro spinal.

Before making any deductions as to the physiological significance of such connections, it is interesting to point out that the inhibitory influences coming from the corpus striatum are transmitted to the spinal cord by means of the rubro spinal tract. What significance does this have? Does it imply that the functions of the corpus striatum and the cerebellum are similar?

While our knowledge of the functions of the red nucleus and rubro spinal tracts has been increased by the experimental work of Magnus and De Kleijn (6), Rademaker and others, nevertheless, the results have by no means been conclusive. Magnus and De Kleijn in their experimental work on thalamus and decerebrate animals expressed their conclusions as follows: (1) if Forel's decussation or the red nuclei are injured then rigidity always develops and the righting reflexes are lost; (2) if Forel's decussation or the red nuclei are not injured then muscle tone remains normal and the righting reflexes are not affected.

Mussen (5) came to exactly opposite conclusions as the result of lesions which were shown to involve the posterior regions of both red nuclei as well as Forel's decussation of the rubro spinal tracts. In another of Mussen's experiments the lesion involved the anterior pole of one red nucleus with probably the field of Forel anteriorly. This produced practically a thalamus animal which Magnus and De Kleijn (6) state should show no disturbance in muscle tone or in righting reflexes, but in this specimen there was marked diminution of muscle tone and at first complete loss of the body righting reflexes, which later were referred only to the side opposite the lesion.

Mussen (5) emphasizes the great difference in experimental results obtained in decerebrate animals from those obtained in normal animals, *i.e.*, with intact central nervous systems, for in Mussen's experiments the animals were kept alive for three weeks, during which time the functions of the central nervous systems had a chance to recover.

It would contribute to our knowledge if we knew more accurately the phylogeny, comparative anatomy and tract connections of the cerebral cortex, corpus striatum, red nucleus and cerebellum. It is well known that the corpus striatum, red nucleus and cerebellum

have an old as well as a new development, but exact knowledge is lacking as to the relative appearance of these older portions. It is probable that the paleocerebellum develops before the paleostriatum, and that the neostriatum develops before the newer portion of the ruber and neocerebellum. According to Kappers (7) a later development consists in the simultaneous appearance of the cerebral hemispheres, the newer portion of the nucleus ruber or the parvocellularis, in conjunction with the expansion of the lateral lobes of the cerebellum.

These factors argue for a successive development according to the needs of the animal for finer differentiation of movement. It would seem that the older connections would subserve a coarser type of movement. This has already been pointed out by J. R. Hunt (8).

Whatever significance the above facts may have it is obvious that the efferent connections of the cerebellum point to certain physiological conclusions. They are that by means of the efferent fibers coming from the cerebellum and transmitted by the rubro spinal and rubro cervical tracts (Mussen (5)) there is synergic control over the trunk, head and neck, upper and lower limbs, the probabilities being that Mussen's rubro cervical tract is largely concerned with the head and neck and to a lesser extent with the upper trunk and upper limbs, and that the cerebello bulbar tracts control synergic movements of the eyes and also of talking, swallowing chewing and eating.

To summarize therefore the evidence so far advanced chiefly from the standpoint of the fiber tracts and their connections, it is obvious both from the afferent as well as the efferent side that there is a very definite order in their arrangement for the purpose of first informing the cerebellum of the state of the entire musculature of the body and of the activity of the associating nervous organisms, and after these impulses are received and integrated wherever synergic effort is necessary the proper impulses are transmitted through the efferent tracts.

The first attempt at cerebellar localization was made by Bolk (9). His method consisted in a study of the cerebellum in a large comparative series, he concluding that several parts recognizable in the mammalian cerebellum had definite functional significance and presented areas of central control over definite motor performances in the body. This work was followed by that of Van Rijnberk (10) who explored the cerebellar cortex by means of circumscribed extirpations of certain of the lobules. The result of his work confirmed Bolk's

hypothesis. These observations have been confirmed in all their essential details by many investigators.

The experimental evidence from stimulation of the cerebellar cortex has been contradictory. Inasmuch as this subject will be discussed in a separate paper in this symposium no extensive reference will be made, with the exception that it is generally held that the cerebellar cortex is inexcitable for movement, and that the central nuclei are. This subject however has by no means been settled. In some investigations by Mussen (5) in which he used the stereotaxic instrument of Horsley and Clarke, he was enabled to get different responses according to the part of the cerebellar cortex stimulated. I witnessed one of his experiments. He has come to the tentative conclusion that each lobe of the cerebellum represents a group reaction, and that the muscular correlation of this group reaction is effected by the combined activity of the folia comprising the lobe. In the lobus centralis for example, combined muscular reactions are found which enable the animal to look upwards, *i.e.*, there is contraction of the posterior neck muscles, elevation of the upper lids and upward movement of the eyes; the nodules give the reactions of the lips, tongue and throat. While these results are tentative and Mussen has by no means come to a definite conclusion, nevertheless they are suggestive and are in line with the theory held by me.

Clinical evidence

There is abundant clinical evidence that there is cerebellar localization. Before presenting my own, I wish to refer to the work of Holmes (11) who studied forty patients in whom there were gunshot wounds of the cerebellum. Of this number twenty-one remained under observation a sufficient length of time to permit of repeated examination and investigation. Holmes came to the conclusion that his observations were only of negative value and that positive deductions could be drawn only for cases controlled by complete anatomical examination, and yet the evidence he presents points to localization. He concluded that the effects of dentate nuclear and cortical lesions differ in no essential particular, but in the latter the symptoms are less intense, less regular, and recover more rapidly. On the other hand, he admits that unilateral lesions produce symptoms which are always limited to the same side. When the vermis was injured the muscles of the head, neck and trunk, including those

concerned in phonation and articulation, were more seriously affected, and the disturbance of function was usually more obvious in mesial than in lesions of one lateral lobe. In comparing the symptoms of unilateral with those of bilateral lesions, the limbs of both sides were affected in the unilateral, but in the bilateral lesions speech was very much disturbed and the muscles of the trunk and neck were very hypotonic and there was difficulty in holding the head in any attitude if unsupported and on sitting up if unaided.

Throughout this excellent paper he points out differences in symptomatology according to the localization of the lesion. On the other hand, Holmes (11) found that cerebellar symptoms were never limited to a segment of a limb or even to one limb. Nearly always both limbs on the same side and the trunk were equally involved. It must of course be remembered that the lesions in his cases were the result of gunshot wounds and therefore necessarily somewhat diffuse.

There are of course many cases reported in the literature of limited lesions resulting either from tumor or abscesses in which the symptomatology has been correspondingly limited. Most of these have been poorly studied although there are excellent exceptions to this rule. It is a curious thing that in the cerebellar literature there never has been and there is not now a consistent attempt on the part of observers to delimit cerebellar symptoms to parts of the body, most neurologists being content with a proper cerebellar diagnosis. It is this lack of effort or failure to attempt regional diagnosis which has retarded our knowledge and progress in cerebellar localization.

In 1914 Mills (12) and I advanced certain views on the functional localization of the cerebellum. In brief we placed the function of coördination of the limbs in the lateral lobes, for the upper limbs in the superior surface, for the lower limbs in the inferior surface; the centers from movement of bilaterally active functions in the vermis, for the head and eyes, tongue, larynx, pharynx in the upper superior surface of the vermis, and the trunkal movements in the remaining part both superiorly and inferiorly. This localization was tentative and was not intended to be conclusive, but it has served as a working scheme and an incentive to demonstrate cerebellar disturbances in parts of the body. What has been our experience since?

The material which I have has been collected over many years. It consists of moving picture records of over fifty cerebellar cases.

In many the diagnosis was confirmed either by operation or by necropsy. (This paper will be followed by a presentation of the pathological material upon which this study is based.) Some of the moving picture records were shown at the International Medical Congress held in London in 1913.

When studying a cerebellar suspect I always approach the problem from two viewpoints: (1) the proper cerebellar diagnosis, and (2) localization of the lesion. I confess that it is not always easy to make a correct diagnosis of cerebellar lesions and yet my mistakes have nearly always occurred when the cerebellar symptoms have been unmistakable, *i.e.*, when the asynergia has involved the entire musculature. In such instances tumors of the third ventricle or pituitary lesions have caused secondary dilatation of all of the ventricles particularly the fourth.

There have been fewer errors in diagnosis whenever the asynergia has been limited to the limbs on one side or to the trunk either alone or in combination with one of the limbs.

From the standpoint of regional diagnosis tumors of the cerebello pontine angle or of the pons offer comparatively little difficulty.

Limited lesions within the cerebellum offer even less provided one is on the lookout for asynergia of one or two limbs or part of the trunk. Such instances are to be found particularly in acute abscesses following middle ear infections. In growing tumors it is sometimes possible to follow successive involvement of the limbs and trunk.

By the kinematograph even in a cursory observation the observer is at once struck with the great diversity in the gait, the station and the movements of the limbs. No two patients have a similar disability. While in most of them there is disturbance in the gait and in the station, yet there are a large number in which the preponderant disturbances are in the legs and to a less extent in the arms only, usually associated however with an accompanying dyssynergia either of the pelvis or of the shoulder.

Another outstanding fact is that in the station or in the gait there is nearly always a preponderant deviation in a given direction. By that I mean that if a patient has a tendency in his station to fall to the right he will rarely fall in any other direction, or if in the gait there is a tendency to go forward or backward or forward and to one side, he will nearly always continue to do so. In the movements of the upper or lower limbs, in the finger to nose or the heel to knee tests,

if there is inward deviation of the upper limb or the leg, such deviation continues throughout the test. The same thing is present in the test for adiadokokinesis, *i.e.*, if there is a tendency of the elbow to turn inwards it remains so throughout the test.

The degree and the nature of the disturbance in the gait and station depend altogether upon whether or not the entire trunk is implicated. It is easily possible to distinguish between the incoördinate movement of the entire trunk, of the lower part or the pelvic girdle alone, or of the upper part or shoulder girdle alone.

In most instances wherever there was a disturbance of synergy in a leg or an arm there was some involvement of the pelvic or the shoulder girdle. The legs were always proportionately more involved than the arms. In many instances however the arm or leg was implicated alone.

All the above points are cited to indicate the fact that disturbances of synergy may be present in parts of the body, *i.e.*, in all the trunk or parts of it, in the trunk together with the upper or the lower limbs, or in one limb alone. Further, that the outstanding characteristic of such movements is either a tendency of the limb or trunk to deviate in a certain direction or fail to go in another direction. All this indicates localization of function.

Certain clinical deductions can be drawn from the station and particularly the gait. Whenever the trunkal movements are involved it can be taken for granted that there is a lesion in the vermis. If the patient staggers backwards the probabilities are that the anterior or the inferior portion of the vermis is implicated as in tumors of the fourth ventricle. As will be described later trunkal disturbances which depend upon lesions of the vermis can be differentiated in so far as they may be limited to either the upper or the lower part. If the upper trunk the lesion is probably in the superior vermis, if the lower trunk, the inferior vermis. If the patient staggers preponderantly in a lateral direction, to the right, the right side of the vermis is probably diseased; if to the left, the left side of the vermis. I did not find disturbance in trunkal movements in lesions which were strictly limited to the lateral hemispheres.

The peculiarity of the gait and station and the direction of the movement in cerebellar cases is capable of many interpretations. In this connection Bárány's (13) views are of the utmost interest. He believes that there are not only centers for direction of movement in

the cortex but also a further representation of muscles within those centers according to the articulation moved.

It is well known that in lesions of the vestibular apparatus a differentiation can be made between the symptoms resulting from involvement of the horizontal and vertical canals. In disturbances of the vertical canals there is produced vertical nystagmus, past pointing in the vertical plane and a tendency to fall backwards or forwards, whereas in lesions of the horizontal canal the nystagmus is mainly horizontal with past pointing of the extremities in the horizontal plane and lateral deviation of the body. Ingvar (14) who has made important contributions to our knowledge of the cerebellum supports Bárány's viewpoint and in addition demonstrated the intimate relationship of the vestibular system with the vermis, the latter receiving practically all the fibers of the vestibular system. He believes that the vestibular impulses are transmitted to the vermis in a similar grouping, *i.e.*, in relation to the horizontal and vertical canals, and that the vestibular innervation of the cerebellar cortex must therefore be arranged on the principle of the different planes of space. He states that lesions of the vermis can to a certain extent be considered similar to the vestibular nerve itself, and that in his experimental animals whenever the posterior lobe—particularly the nodules and uvula—were removed, the animals had a remarkable tendency to fall backwards, but if the anterior lobe or the vermis was ablated, the animals showed a tendency to fall forwards.

Ingvar (14) regards the cerebellum as a reflex organ which preserves the static and dynamic equilibrium of the organism and that this conception better than any other hypothesis explains the anatomical and histological uniformity of the cerebellum in the whole vertebrate series, and is in accordance with the clinical symptoms of cerebellar disease.

This is an interesting conception but it does not stand the test of clinical facts. For example, in discussing how falling backwards is produced he states "that if destruction of the posterior lobe elicits falling backwards we must ascribe to the posterior lobe the faculty of eliciting in some way the necessary muscular synergies that are necessary to bring about the falling backwards." Further, "that the anterior lobe was related mainly to regulating the motor functions necessary to maintain the equilibrium of the body and preventing the body from falling forwards, whereas the posterior lobe played a rôle

in maintaining the equilibrium backwards." These are contradictory statements. To the posterior lobe cannot be ascribed the dual duty of maintaining the equilibrium of the body and preventing it from falling backwards, and if diseased "eliciting in some way the necessary synergies which are necessary to bring about the falling backwards."

It seems to me that this reasoning is faulty for it ascribes to a part of the cerebellum which has been destroyed a positive function. Further he assumes that the cerebellum is alone concerned in equilibration, ignoring, first, the fact that the uninjured portions of this organ have their work still to do, and secondly, that in every posture or movement the cerebro spinal system and the striatal system are equally concerned.

I believe that the cause of the deviation of a trunk or a limb is a destruction of certain synergic units and that whatever movement occurs is the result of the activity of the cortical and mid-brain levels and the uninjured portion of the cerebellum expressed through the lowest motor level in the spinal cord.

In this connection I wish to call attention to a very interesting observation regarding the cerebellar gait. In a patient who constantly staggered backwards, when asked to run around on his hands and feet like an animal, he did so with ease. When trying the same experiment with other patients who have trunkal disturbances, they were able to walk on their hands and feet according to the degree of disturbance of the trunk.

THE NATURE OF CEREBELLAR SYMPTOMS

My moving picture observations originally reported in 1914 with Mills (12) and further elaborated by the studies of Tilney and Goodhart (15), show beyond question that synergizing of muscular units is the fundamental function of the cerebellum, and that in lesions of this organ asynergia is the fundamental symptom of cerebellar disease. By ultra rapid motion pictures and by a graphic record Tilney and Goodhart showed that synergia is dependent upon two factors, (1) the establishment and maintenance of synergic muscular units throughout the body, and (2) the establishment and maintenance of coördination between the synergic units in the performance of complex acts. Throughout the entire body the muscles are arranged in unit groups each unit consisting of agonists and antagonists. These groups do not operate as antagonists but as synergists. In a synergic

unit two factors may be recognized, (1) the dominant element which determines the direction of the movements, and (2) the check element which works constantly with the dominant in order to provide the necessary limitation so that the resultant movement may at no time be excessive but always exactly adapted to the purpose in hand. The larger the movement the greater the number of synergic units employed. In every muscular act there are two phases, the kinetic and the akinetic. The first produces a motion, the second maintains a fixed position under active contractions of the muscles, such as for example, in reaching for a glass and in holding it.

If there is a lesion in any part of the cerebellar apparatus there is necessarily produced a disturbance or destruction of the association between agonists and antagonists, and the resulting movement must necessarily be incoördinate or asynergic.

Here arises a fundamental difference in opinion as to how the incoördinate movements are produced. André Thomas (3) advances the theory which he called anisosthenia, in which he claims that in partial lesions of the cerebellum there may be a loss of tone in some muscles with relative hypertonicity in their antagonists, *i.e.*, that there may be hyposthenia in one group and hyperasthenia in another. This same theory but couched in different language is held by most writers on the cerebellum and is used to explain most of the symptoms of deficit, *i.e.*, the station, gait, dysmetria, hypermetria, adiadokokinesis and so forth.

It is obvious that a destructive lesion cannot produce any positive symptoms. If for example there is a lesion of the right lateral lobe there will be produced an asynergia of the homolateral limbs, but this is not because of the activity of the destroyed area for this has ceased to function, neither can the remaining uninjured portion of the cerebellum compensate for the destroyed part for it has its own function still to perform.

My own view is in accord with that of Hughlings Jackson (16) that the cerebellum cannot and does not act alone, that it acts always with the other motor levels in the cerebral cortex and in the mid-brain in conjunction with the lowest motor level in the spinal cord; that if any lesion occurs in the cerebellum the negative symptom consists in the inability of the patient to perform muscular movements in a coördinate or synergic manner, and that whatever the patient is able to do, in other words, the gait, the station, the particular movements of the

arms which are described under various terms such as hypermetria, dysmetria, and so on, is the result of the activity of the other motor levels, *i.e.*, the cerebral and the midbrain levels acting through a common pathway upon the lowest motor level in the spinal cord.

With this assumption it is obvious that whatever manifestations a patient has depend upon the extent and location of the lesion, the larger the lesion the greater the extent of deficit, *i.e.*, the inability to perform an act in a coördinate or synergic manner and the greater the positive symptoms or the effort of the other motor levels to compensate for the loss of cerebellar function. In a small limited lesion, for example in a lateral lobe, there need be only disturbances limited to an upper or a lower limb, whereas if the lesion is in the vermis the disturbances may be in the trunk as well as the upper and lower limbs again depending upon the extent of the lesion.

There is also a difference in symptomatology according to how the lesion is produced. In acute lesions certain symptoms will be present which are compensated for in a gradually developing degenerative process or in a tumor. There is no doubt that in acute lesions such as described by Holmes (11), and in traumatic surgical lesions, there is very marked atonia and even weakness in movement, but neither of these symptoms are present in more chronic or tumor lesions. This undoubtedly accounts for the discrepancies in the clinical observations and it is because writers on the subject have failed to take this into consideration that many of the discrepancies in the clinical descriptions have arisen.

Admitting that *atonia* is present in acute lesions, how is it produced? Ingvar (14) in 1918 suggested that all the various cerebellar symptoms were consequent to a disturbance of muscular tone following his conception that the cerebellum was an organ regulating the static and dynamic equilibrium of the body. Similar views were expressed by Hunt (8) and by Walshe (17), who maintained that neurologists use the term tone or atonia incorrectly. Muscle tone according to him should be used in the sense in which Sherrington employs it, *i.e.*, the basis of posture and coördinated posture adaptation. By atonia he understands a loss or impairment of the tonic posture reactions of the normal musculature. He then concludes "may we not suggest that the cerebellum is the organ through which the cerebral motor cortex influences posture activities and regulates posture in the interest of coördinated purposive movement?" Is not this conception another

way of stating that the cerebellum is the organ through which the cerebral motor cortex influences synergic movement?

Asthenia or weakness is undoubtedly present in acute lesions. Holmes gives an excellent description of this symptom and I have seen it in cerebellar injuries following operations. Such asthenia or weakness in one case under my observation lasted for at least two months and gradually disappeared. It is not however present in slowly developing lesions. Various explanations have been offered for this symptom such as pressure on the motor tracts, co-existing cerebral foci, atonia and so forth. Holmes considers it a primary and immediate symptom of cerebellar injury and makes the additional observation that it is probably pronounced only when the cerebellar nuclei are involved and that the fatigability is dependent upon this asthenia.

I believe however that another explanation can be offered for the presence of both atonia and asthenia, and that is von Monakow's new massing theory of diaschisis. In common with the other motor levels any acute lesion always produces two fundamental symptoms, (1) some impairment of movement, and (2) disturbance of tone.

Cobb (18) in a recent review summarizes his views on tone as follows: that there are four levels of integration (1) the main tone posture centers in the medulla closely related to the vestibular apparatus; (2) the red nucleus and its connections in the mid-brain which control tone; (3) a more complicated control in the basal ganglia; (4) the cortical motor centers which control tone only by abolishing it, when they wish to impose special movements in the place of postures, and concludes that "at present the better evidence points to the simpler explanation: that tonus is a beautifully graded series of proprioceptive reflexes, continuously and unconsciously playing its part in our every motor act. By its remarkable specificity it moulds our individual muscles; by its universality it controls our postures." When considering how intimately the cerebellum is bound up with all of these levels it is conceivable that in acute lesions there is a temporary disturbance of their function with the production of atonia and of weakness depending upon the extent of the lesion.

The presence of *nystagmus* and of other ocular disturbances in cerebellar lesions has been disputed. Holmes however believes that it is extremely probable that nystagmus is due to damage of the cerebellum alone. He states that it varies according to the severity of the injury and that it may be partly dependent upon the localization

of the lesion, though he is unable to state definitely that this is so. He concludes that it seems that each half of the cerebellum has an influence not only on conjugate movement of the eyes towards the same side, but also on vertical movements and on further deviation towards the opposite side, and that it is closely allied to the influences which come from the labyrinth.

Holmes (11) describes five cases in which skew-deviation was observed, *i.e.*, the homolateral eye was directed downwards and inwards, while the other looked upwards and outwards. This is only a temporary symptom.

Nystagmus in cerebellar lesions has been described by a number of observers but it is not a common symptom at least in chronic lesions. I have seen a number of lesions involving the cerebellum in which nystagmus was always more marked on deviation of the eyeballs towards the side of the lesion, but localization was difficult. It is a common symptom following cutting, surgical operations.

I have seen only one instance of skew-deviation and it was present only during a so-called tonic spasm which will be described later.

I do not believe however that *astasia* is present in acute lesions. What is commonly described as *astasia* is the result of a disturbance of synergy.

The symptoms resulting in acute lesions therefore differ from those which are present in chronic lesions in three things, the presence of atonia, asthenia, and to a less extent nystagmus, these symptoms however being present only for a time. They gradually disappear the time depending upon the extent of the lesion. In every other way the symptoms in acute lesions are similar to those present in chronic lesions, keeping in mind always that the extent and location of the lesion control the symptomatology.

It is not the purpose of this paper to discuss extensively all the symptomatology of cerebellar lesions. I wish to comment however upon certain aspects which are well brought out by kinematographic studies.⁴

Abnormal position of the head. In only two instances have I observed any deviation of the head to one side and they were in cerebello pontile angle tumors with diplopia. Correction of the same

⁴ For a full description the reader is referred to the original paper by C. K. Mills and T. H. Weisenburg: Cerebellar symptoms and cerebellar localization, *J. Amer. Med. Assoc.*, lxiii, 1813-1818, November 21, 1914.

with glasses removed this deviation. In every other instance the position of the head was in line with that of the trunk.

Gait. A cerebellar patient when asked to walk across the stage will take advantage of every sense so as to correct his difficulty in walking. The gait is distinctly modified whether the eyes are open or shut or by sounds. When walking with the eyes open the deviation will be at once corrected or with the eyes shut by the sound of the voice. The cerebellar gait is best demonstrated with the eyes blindfolded and without any sound.

When the entire trunk is involved there is the greatest disturbance in the gait and in the station, and frequently such patients are unable to stand up, or in attempting to walk will fall in almost any direction. On the other hand, if the pelvic girdle is involved alone the trunk is held rigidly erect and the legs are pushed forward from the pelvis giving the impression that the trunk goes after the legs. In extreme cases the patient cannot walk even with help and when assisted the trunk is held rigid and the legs are thrown out in almost any direction. In such cases the upper limbs are usually held partly outstretched and semiflexed at the elbows in an attempt to balance. On the other hand, if the shoulder girdle alone is implicated the patient usually stand very well and walks almost normally although he has a tendency to spread his legs apart, but in his station he is likely to fall and when walking will lurch usually in a certain direction, giving the impression that the trunk leads and whichever way it goes the legs follow.

An excellent way to differentiate between pelvic girdle and shoulder girdle asynergy is to have the patient get up from a recumbent posture. In his efforts to do so while his hands and feet are extended, if the pelvic girdle is involved alone there is a distinct to and fro swaying of this part, the shoulder girdle remaining stationary. The contrary is present when the shoulder girdle is involved.

The nature of the movements of the arms and legs. This varies considerably. There is a slowness in the initiation of the movement but it is not present in all cases. After the movement starts it is slower than normal although in some it is faster and in nearly all instances there is an overshooting. There is so much variation however in the movements of the limbs that my general impression is that the tempo depends upon the extent of the lesion, the larger the lesion the slower the movement and the greater the oscillations and the overshooting. In smaller lesions the movements are more rapid as if the patient is making a conscious effort to overcome the disability.

In kinematographic studies the nature of such movements is beautifully shown. It does not matter what test is used the movement is always the same although it depends upon the acuteness and extent of the lesion. I believe that such symptoms as dyssynergia, hypermetria, dysmetria, adiadokokinesis, the rebound phenomenon, and all other symptoms which are used in the description of cerebellar lesions, depend upon the fundamental symptom, *i.e.*, the degree of asynergia present. If this were recognized and adopted a great service would be rendered to cerebellar symptomatology and there would be an abandonment of the attempt to explain each one of these symptoms by some special disturbance. For many years both in teaching and in writing on this subject I have abandoned this complicated terminology and have described all symptoms of cerebellar deficit no matter how obtained, under the term of asynergia, describing however how obtained and the extent of it.

Tremor is not a distinct symptom of cerebellar deficit. It can be brought out in every patient but it is due to disturbance of synergy and depends upon the extent of the lesion.

Catalepsy. I was unable to demonstrate this in any of my patients. In putting them on their backs with the arms held upwards and the legs flexed at the knees, it was noticeable that the limbs on the injured side always drooped first, quite the contrary of what is to be expected from Babinski's description.

Fatiguability. It has seemed to me that in most of the cerebellar cases it is possible to demonstrate a fatiguability in the limbs of the affected side. In placing a patient on his back and asking him to fold his arms and attempt to assume a sitting position, the legs on the involved side always give way perceptively. In fact this is a constant observation and I always look for it in cerebellar patients. Persistent efforts such as walking, holding weights or moving the arms and legs always show an early fatiguability, but it is not because there is weakness of the limbs.

Facial and emotional expression. This is not as a rule disturbed unless there is difficulty in articulation and phonation when the face seems less mobile and talking more of an effort.

As a rule the emotional expression is not involved but here again it seemed to me that whenever there was difficulty in talking the face appeared to have less expression in it and that it was difficult for the patient to laugh. In one patient described by Mills, in whom

there was a thrombosis of the superior cerebellar artery on one side with a lesion extending into the dentate nucleus, there was complete loss of emotional expression on one side of the face although the muscles could be used for every other purpose.

Tonic spasm. This was seen by me only in one patient. It was in a man of twenty who had a left cerebello pontile angle tumor about the size of a hen's egg, which grew from the auditory nerve and extended downwards through the foramen magnum along the medulla. The lesion was diagnosed in life and confirmed by necropsy. I saw one seizure which began by a turning of the head to the right, then a retraction backwards with the vertex pointing to the left. Coincidentally the left arm was lifted above the head, the arm flexed at the elbow, wrist and fingers deviated outward and downward. At the same time the left leg was lifted from the bed and extended straight outwards. The right limbs were not moved but were rigid. The left legs were in a tonic spasm and there were no twitchings.

Coincident with the deviation of the head both eyes jerked to the right. The movements began about the mid-point, the quick component being to the right. The nystagmoid jerkings were followed by a skew-deviation, *i.e.*, the right eye was up and out, the left down and in.

During the attack it was possible to obtain a bilateral extension of both toes in plantar stimulation. The patient was stuporous but was able to execute some commands. His pulse was slow, about 60 to the minute. He was generally pale and respiration was rapid. The right pupil was larger than the left. After the attack it came to normal. The Babinski reflex disappeared on the right side in about ten minutes, on the left it persisted.

The duration of the entire attack was three minutes. The skew-deviation lasted five minutes and disappeared slowly.

The maintenance of the deviation of the head to the right and backwards and the tonic condition of the left limbs lasted about three minutes. It was impossible to turn the head in any direction during the attack. Afterwards deviation of the head did not produce contracture of the limbs.

This very interesting case presented a tonic spasm in which the position of the head and the limbs on the left side was very similar to the description given by Hughlings Jackson (16), excepting that the fingers were not clenched and that the spasm was unilateral, *i.e.*,

involved the limbs on one side. The simultaneous extension of the left limbs with the deviation of the head and neck to the right is an example of the Magnus and De Kleijn reflex.

The tumor which was a neuroma growing from the auditory nerve was quite large and cystic, and did not directly involve the cerebellum. The sensory fifth, sixth and seventh cranial nerves were involved by pressure. An interesting feature however was the fact that the tumor extended into the internal auditory meatus and was very firmly attached. The specimen was studied by Dr. E. A. Case who reported it as follows:

A part of the petrous portion of the temporal bone was decalcified and the auditory nerve dessected out as far as its division into the cochlear and vestibular branches. The rest of the bone was imbedded in celloidin. The preparations were not as satisfactory as one could wish, and it is well to remember that the structures of the internal ear disintegrate rather early unless promptly and thoroughly fixed. The nerve was most certainly involved as far as its cochlear and vestibular branches, as it had the same appearance as the portion found attached to the internal auditory meatus. Beyond this point we could not go. In the sections of bone, no normal cochlear tissue was found and, in the spaces taken for this structure, there was destruction of the normal architecture. The semicircular canals did not appear to be involved to the same extent.

While our study was not as satisfactory as it should be, yet I feel that we are justified in believing that the nerve was involved up to its division into the cochlear and vestibular branches and that there was an associated degeneration of the structures of the internal ear.

I do not know how to interpret the presence of the tonic spasm and the skew-deviation. In Jackson's case there was a tumor of the middle lobe of the cerebellum. Here the cerebellum implicated was by pressure. The involvement of the vestibular and auditory nerves must of course be taken into consideration.

CONCLUSION

1. The function of the cerebellum is to synergize all motor activity. The cerebellum never acts alone. Its activities are correlated with the other motor levels in the cerebral cortex, mid-brain and spinal cord.

2. Lesions of the cerebellum produce positive and negative symptoms. The positive symptoms consist in an inability to perform synergic movements properly. The negative symptoms, *i.e.*, the difficulty in movements whether of the trunk or limbs is the result

of the activity of the other motor levels in the cortex and mid-brain acting through the spinal cord.

3. There is functional localization in the cerebellum. In the vermis are represented the synergic activities of the trunk; in the superior vermis the movements of the shoulder girdle or the upper trunk; in the inferior vermis the pelvic girdle or the lower trunk. Synergic activities concerned in talking and movements of the eyes are located in the vermis in all probability in the superior vermis. Synergic control of the limbs is in the lateral hemispheres, for the upper limbs in the superior portion, for the lower limbs in the inferior.

4. There are no centers for deviation in the cerebellum.

5. The fundamental defect symptom of a cerebellar lesion is asynergia. Such symptoms as dysmetria, hypermetria, ataxia, adiokokinesia, are all the resultants of disturbance of synergy.

6. The recommendation is made that the complicated terminology used to describe symptoms of cerebellar deficit be abandoned and that instead actually symptoms be described in terms of loss of synergy.

7. The extent of the synergic disturbance present depends upon the nature, extent and localization of the lesion.

8. In acute lesions atonia and asthenia are present. This probably results from a temporary disturbance of the other motor physiological levels. In all other ways symptoms of acute and chronic lesions are similar.

9. In every cerebellar patient an attempt should be made to delimit cerebellar symptomatology to parts of the body with a view to localization of function.

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CHAPTER XVIII

DISTURBANCE OF VOLUNTARY RHYTHMIC MOVEMENTS IN CEREBELLAR DISEASE (ARRHYTHMOKINESIS)

F. I. WERTHAM, M.D., AND R. S. LYMAN, M.D.

INABILITY to perform rapid alternating movements was first described by Babinski in 1902. He believed that this symptom is pathognomic of cerebellar disease and that it is based on a special function which consists in the association of an excito-motor and a regulating action. Clinical experience has shown that adiadochokinesis may also occur in a variety of other conditions, such as in Parkinson syndrome, Friedreich's ataxia, spastic paralysis, in hemiplegia (Lewandowsky, 1910), etc. The fundamental principle behind the failure to repeat these movements in quick succession can of course not be identical in lesions of such different origin and localization. The differentiation of the underlying mechanism in cerebellar disease from that in other disorders meets on common ground with these studies on the repetition of voluntary rhythmic movements.

The test of diadochokinesis consists of the repetition of voluntary rhythmic movements at the maximum speed of which the individual is capable. It can be disturbed chiefly with regard to speed and with regard to regularity. Although a person may be unable to perform alternate movements rapidly, he may still be able to make successive movements with a definitely regular rhythm at his own speed. From this point of view the ability to perform correctly voluntary successive movements of a definite rhythm, but not at a prescribed speed, was examined in a number of patients showing the symptom of adiadochokinesis.

APPARATUS

The apparatus used was very simple. A telegraph key was equipped with a rather large ebonite plate instead of the usual sending-knob, so that a patient with ataxia even when deviating laterally would still strike the plate and thus effect contact in the circuit with every

vertical movement. The tapper key was connected with a signal-marker which recorded on an ordinary smoked drum above a time-marker registering each second (fig. 188).

PROCEDURE

The observer tapped a definite rhythm on the table or on a book. In most experiments a simple rhythm was used. This was repeated until the patient had learned it well enough either to tap it on the table or to sing it. The patient was then asked to reproduce it with one hand on the sending-key. In a number of cases a more compli-

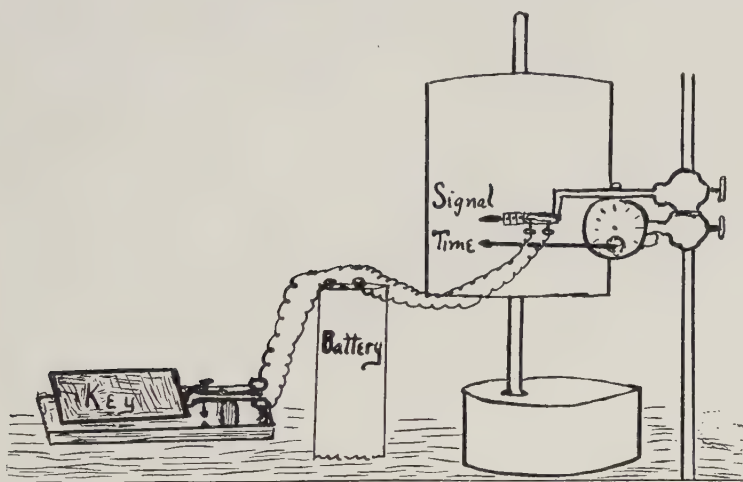


FIG. 188. Diagram of apparatus. Telegraph key with ebonite plate instead of usual sending knob. Signal and time-marker recording on smoked drum.

cated rhythm was tried. As a rule each subject was allowed to choose his own rate, although occasionally the patient was asked to increase the speed, in order to bring out the characteristic disturbance more clearly. The repetition of these voluntary rhythmic movements was carried out with each hand separately while the other hand was kept comfortably at rest. Then simultaneous repetition of the rhythm was tested with both hands, one striking on the tapper key and the other on the table or on a book. Cases which showed adiadochokinesis as a unilateral symptom were especially selected. The rhythmic movements were performed first on the sound side so that the psychological

ability to appreciate and reproduce the rhythm was established. The result was then compared with tapping the same rhythm with the hand on the affected side. Right and left handedness as well as previous musical training were noted in each case. The arm was not supported in any test in order to allow associated movements at the elbow, if present, to reinforce the disturbance.

EXAMPLES OF TYPICAL RECORDS

Patients with a variety of clinical conditions were examined in this way but only those were included in this series in whom the clinical diagnosis was clear. A characteristic disturbance in the reproduction of these movements was found in a number of cases but it did not necessarily go hand in hand with the degree of adiadochokinesis. It was found, however, and at first quite unexpectedly, only in patients with cerebellar disease.

From this series a few typical curves will illustrate the characteristic findings of correctly performed voluntary rhythmic movements and of the disturbance of their execution (fig. 192).

Case 1. Patient, boy, age 10 years. Did not play piano; right handed; had adiadochokinesis. Clinical diagnosis; Cerebellar tumor verified by operation. Tumor extended more into the right than into the left hemisphere but it crossed the midline involving both hemispheres. Case of Dr. Charles Bagley, Baltimore (fig. 191).

Case 2. Patient, girl, age 10 years. Did not play piano; right handed; slight adiadochokinesis on right. Clinical diagnosis: Cerebellar tumor, verified by operation. There was a soft tumor projecting between the two cerebellar hemispheres. Case of Dr. Charles Bagley, Baltimore (fig. 190).

Case 3. Patient, man, age 35 years. Clinical diagnosis: Metencephalitic Parkinson syndrome of six years duration. Marked Parkinsonian attitude with little tremor (fig. 189).

FIG. 189. Patient with metencephalitic Parkinsonism. Rhythm slowly but correctly repeated.

FIG. 190. Another patient with cerebellar tumor. Same rhythm, only twice correctly performed.

FIG. 191. Record from patient with cerebellar tumor. Simple rhythm clearly reproduced three times and then becoming increasingly unrecognizable.

FIG. 192. Normal control. Correct performance of a simple and a more complicated rhythm. Time in seconds.

FIG. 189

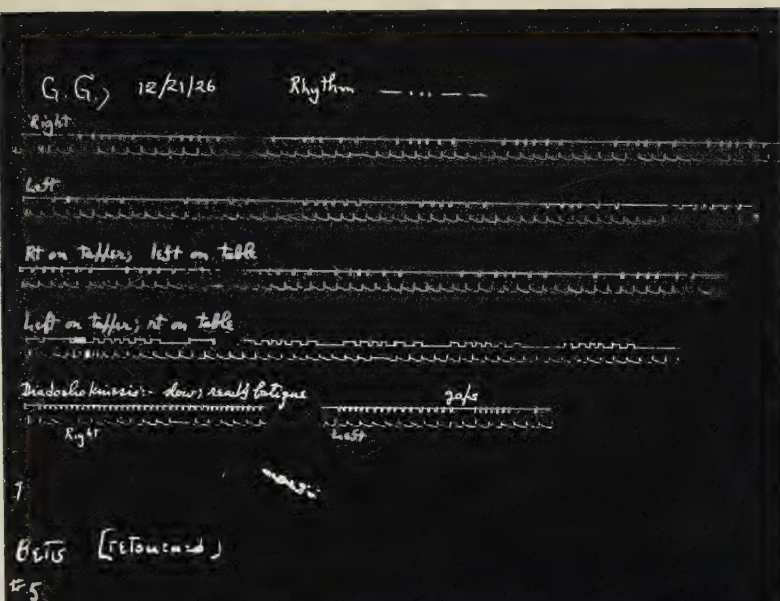


FIG. 190

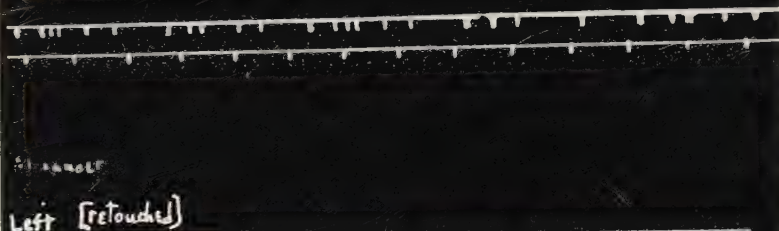


FIG. 191

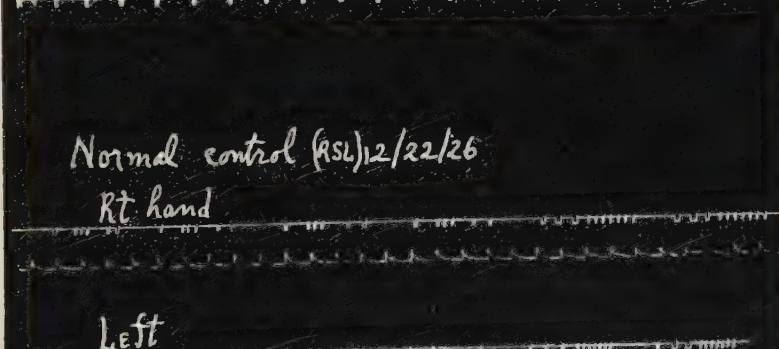
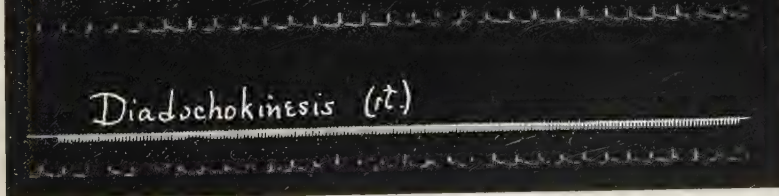


FIG. 192



DISCUSSION

Similarities between adiadochokinesis and arrhythmokinesis

It has long been known that the performance of diadochokinesis can be influenced by a number of factors, minutely analyzed by Gordon Holmes (1917). Practically all of them affect also the performance of rhythmic movements. For example, the more complex the movement, the more pronounced the disturbance. Merely tapping a key is of course a very simple movement, involving action at only one joint. If, however, in testing for adiadochokinesis, movements at two or more joints are made simultaneously, *e.g.*, opening and closing the fists, the facility of carrying out either test is distinctly impaired. Further, any increase in the resistance, against which the movement is made, rapidly inhibits the correct performance of alternating movements. In our experiments the subject was made to pull against elastic bands and the difficulty in producing the simple rhythm changed in proportion to the tension of the elastic bands. A further similarity between adiadochokinesis and the disturbance in the repetition of rhythmic movements is the following: In testing adiadochokinesis the characteristic disturbance is found to be more pronounced or at times it can only be elicited at all by simultaneous use of both hands. Our curves show very clearly that this is true in testing rhythmic movements as it is in testing rapid alternate movements. Another factor influencing diadochokinesis and the repetition of rhythmic movements independent of speed appears on mere observation of continued repetition. A patient may start correctly and after an initial break in rhythm the errors then pile up one after the other until the rhythmic pattern is completely lost.

Difference between adiadochokinesis and arrhythmokinesis

Those features on the other hand which distinguish the production of rhythmic movements from the performance of rapid alternate movements, are the main point in the contribution of our studies. Holmes has shown clearly with graphs that, whereas both speed and regularity were impaired in adiadochokinesis, the conspicuous phase of the disturbance in cerebellar disease occurred at "the turn," where one movement would stop and the alternate movement would begin (fig. 193). In the present studies just this phase of greatest disturbance, namely "the turn," has been made use of. For the production of

rhythmic movements depends on and emphasizes this "turn," because starting and stopping, initiating and relaxing demand even more control at the "turn" in these rhythmic movements than is called for in the simple repetition of alternate movements at regular intervals. In diadochokinesis movement at maximum speed is implied; in testing alternate rhythmic movements the speed can be varied. The rhythmic movements can be done correctly at different speed, slowly or fast. Interrupted sequence, especially when carried out relatively slowly, naturally gives the patient less sense of fatigue than the test of diadochokinesis where he is pushed to continue at

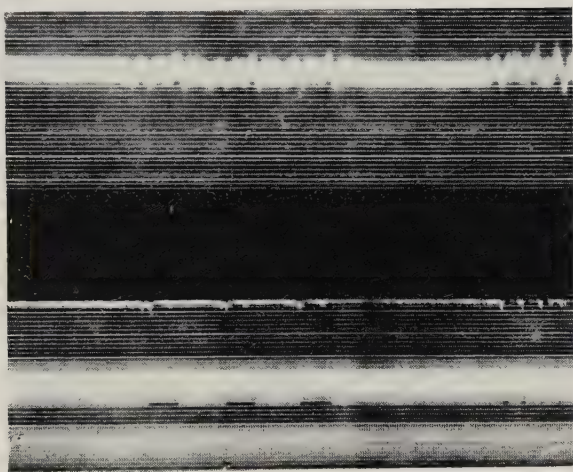


FIG. 193. From Holmes, *Brain*, xl, 1917

maximum speed with maximum effort. The element of fatigue enters not only into the repetition of movements in cerebellar disease but also into the repetition of movements in any other conditions. Consequently reduction of this fatigue reduces a factor present in adiadochokinesis which is not characteristic of cerebellar disease alone. These differences between adiadochokinesis and inability to do rhythmic movements seem to be well defined. Also the inability to do rhythmic movements may according to our observations be present or absent in patients showing marked adiadochokinesis. For these reasons this phenomenon is sufficiently distinct to warrant separate consideration and the introduction of a special term. We have spoken of this test in analogy to the term adiadochokinesis—as arrhythmokinesis.

Definition of arrhythmokinesia

We understand by arrhythmokinesia the inability to perform voluntary rhythmic movements independent of speed, tested most conveniently by tapping. This disturbance occurs on a neurological level. In order to test it accurately the constitutional differences in rhythmic ability both as regards the intake of rhythm (sensory rhythmic ability, optic and acoustic) and execution of the rhythm (motor rhythmic ability) have to be taken into account. It may be recalled that Beethoven, a genius of rhythm, could not dance to music. The



FIG. 194. Electromyogram: normal subject. Record from flexor muscles of forearm at top; from extensors of forearm just below black band; below that signal on tapping telegraph key; time at bottom, $\frac{1}{40}$ seconds. Read from right to left. Note regularity of excursion and synchronous action of strings with records of tapping and absence of movement of strings between taps.

ruling out of the psychological factor can be accomplished with the best degree of certainty by making sure that the subject can reproduce the rhythm correctly, either with the unimpaired limb in unilateral cases or by singing, in such a way that the observer can easily recognize the rhythmic pattern. This requires good coöperation on the part of the patient, which varies of course considerably. We found in a number of children that the rhythm was very easily learned. In some adults the learning process was slow. Improvement with practice, fatigue and, of course, the presence of involuntary hyperkinetic symptoms (*e.g.*, tremor in Parkinson syndrome) have to be carefully considered.

ANALYSIS BY MEANS OF ELECTROMYOGRAMS AND ATTEMPT AT PHYSIOLOGICAL EXPLANATION

It seems likely that the mechanism of the physiological disorder underlying arrhythmokinesis is fundamentally the same as that underlying the adiadochokinesis of cerebellar disease. Conclusive proof is not provided in this paper, but very suggestive results have been obtained from an attempt to get electromyogram from the flexors and extensors of the forearm—the opposing groups which give the alternate movements of tapping on a telegraph key. It appears from the records obtained in this way that inability both to tap rapidly and regularly and also to carry on correctly movements at a definite though slower rhythm, can be at least partially explained.



FIG. 195. Electromyogram: patient with multiple sclerosis; cerebellar signs pronounced. Arrangement as in figure 194; size of picture much reduced. Reading right to left, rhythm correctly performed to arrow-mark, then becoming unrecognizable. Note greater irregularity in excursions and time of galvanometer records and inability of strings to come to complete rest between taps.

In the normal subject (fig. 194) immediately preceding the movement of flexion which is recorded with a tap on the signal-marker there is a brief twitch of the string leading off from the flexor group. Its duration is short, the amplitude is small, and the period following the flicker shows an almost immobile string until immediately before the mark of the next tap. The same may be said to hold for the record of the string from the extensor group of muscles except that the duration of its twitch is even less in amplitude and it follows definitely and regularly immediately after each signal mark.

In a patient with multiple sclerosis having pronounced signs of cerebellar ataxia in arms and legs, the electromyogram taken under identical conditions presents a quite different picture (fig. 195). Looking first at the signal-marker it is seen that the rhythm starts correctly (...-). Then an incomplete signal is inserted barely

recognizable on the record. After that the rhythm becomes quite indistinguishable. The string connected with electrodes over the flexor muscles gives an initial twitch immediately before the first signal mark. Thereafter it oscillates at uneven intervals and with varying amplitude before succeeding taps on the signal-marker and between those mechanical signals. The string from the extensors is even more irregular in amplitude and in its time relations with the movements of the tapper-key. From this record alone it is difficult to see how the rhythm could have been tapped out even as well as it was. The outstanding features then, in patients with arrhythmokinesis, for which complete explanation is not yet at hand, are irregularity in amplitude of action currents, their continuation long after the mechanical movement has apparently stopped and considerable lack of synchronous relations between flexor and extensor action currents.

CONCLUSION AND SUMMARY

An inability to repeat correctly voluntary rhythmic movements independent of speed is described, which can be conveniently tested by tapping. It is associated with *adiadochokinesis* but has to be distinguished from it both physiologically and clinically and may be designated as *arrhythmokinesis*. In these studies it has been found typically only in cerebellar disease and not in the other cases with marked *adiadochokinesis*, such as Parkinson syndrome and Friedreich's ataxia. *Arrhythmokinesis* seems to be more characteristic of cerebellar dysfunction than is *adiadochokinesis*. In testing *arrhythmokinesis* in cerebellar disease it was found that, when both hands tapped, simultaneously, the typical disorder was increased, whereas in Parkinson syndrome with *adiadochokinesis* the simultaneous tapping with both hands seemed to improve the rhythm. Electromyographic studies of the muscle groups involved have so far established a considerable lack of synchronization between the agonists and antagonists in *arrhythmokinesis* and in the *adiadochokinesis* of cerebellar disease. Demonstration of *arrhythmokinesis* is a simple clinical test. It seems to be an easy way of eliciting impairment of cerebellar function, especially striking in bringing out differences between the two sides in unilateral cerebellar lesions.

The occurrence and explanation of *arrhythmokinesis* in cerebellar disease seems to point again to Gordon Holmes' summing up of the cerebellum as a motor reinforcing organ which "sets" or "tunes" the

segmental motor mechanisms, so that they respond immediately, effectively and with appropriate force to cerebral impressions. For this accurate response, is of course, indispensable in executing rhythm correctly and a disturbance of rhythmic movements must result from inefficient response to cerebral impressions such as occurs in cerebellar disease.

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CHAPTER XIX

THE RELATIONSHIP OF EYE MUSCLES TO SEMICIRCULAR CANAL CURRENTS IN ROTATIONALLY INDUCED NYSTAGMUS

JOHN FAVILL, M.D.

THE original observations by Ewald after producing endolymph movement in pigeons laid the foundation for much subsequent controversy and conflicting opinion regarding human semicircular canal currents and eye muscle responses. Ewald (1) concluded that: first, excitation of any single canal can produce nystagmus only in a plane parallel with the plane of that canal; second, the relation between the direction of the endolymph movement in any canal and the direction of the resulting nystagmus is definite and constant; and consequently, third, by reversal of the endolymph movement in any canal the direction of the induced nystagmus can be reversed.

Three major difficulties have obscured the situation so far as the human mechanism is concerned. First, it has been argued that human endolymph cannot move in currents. Second, there has been confusion as to the positions in which the human canals lie. Third, while accepting the idea of endolymph currents, opinions have differed as to the assignment of certain eye muscles to the vertical canals.

Regarding the claim that human endolymph does not move, it is to be noted that evidence has been presented from minute models of the human system both supporting and opposing the probability of movement. Endolymph movement however is the best explanation of the following facts: (1) horizontal nystagmus produced after rotation in one direction is reversed when rotation has been made in the opposite direction; (2) horizontal nystagmus produced by douching with the head 60 degrees back is reversed when the head is bent forward through 180 degrees without further douching; (3) horizontal nystagmus produced by douching with hot water is reversed when cold water is used without change of head position. In view of this,

and because no one has seen human endolymph fail to move on stimulation, such movement must still be regarded as possible.

The second and third difficulties above mentioned may be vividly illustrated by the following contradictory opinions:

Ruttin (2) assumed the anterior vertical canals to be practically in a transverse plane of the head and the posterior verticals practically in sagittal planes. He therefore assigned the oblique muscles to the anterior verticals and the superior and inferior recti to the posterior verticals. This has been the point of view taught in Vienna since then.

Lemere (3) claimed that the anterior vertical canals were much more nearly in sagittal planes and the posterior verticals more nearly in a transverse plane. He accordingly assigned the superior and inferior recti to the anterior verticals and the obliques to the posterior verticals.

Thus it seems to have been considered *a priori* a necessity to assign all the oblique muscles to similar vertical canals in each labyrinth.

Text-books on anatomy, physiology and otology are now generally agreed that the anterior vertical canal of one labyrinth lies in a plane parallel to that of the posterior vertical canal of the other labyrinth and that such planes make angles of 45 degrees with the sagittal plane. These planes of the vertical canals are perpendicular to the plane of the horizontal canals which slopes down and back about 30 degrees from the horizontal plane. If the head is placed about 30 degrees forward, the horizontal canal plane is now horizontal and the vertical canal planes are vertical. Figure 901 in Spalteholz (4) illustrates this description of the vertical canal planes and was made from an actual preparation.

Hence, in the head positions used for obtaining rotary nystagmus after rotation (120 degrees forward or 60 degrees back) and in those used for obtaining vertical nystagmus (90 degrees to right or left shoulder), all four vertical canals should receive an equal quantity of stimulation. As each is thus at 45 degrees with the plane of rotation, each receives one half of a maximum possible stimulus for current production.

The fact that each vertical canal at its mesial end joins its fellow in a common crus before entering the utriculus led to the belief that current in one canal toward this crus necessitated current in its fellow also toward the crus, and vice versa (5).

In a previous publication, I (6) showed, from experiments with glass

models of the canals, that in the position for obtaining vertical nystagmus the current should pass the common crus, one canal current flowing toward it and the other away from it. I did not know at that time that Quix (7) had previously made this suggestion in a Dutch publication. Using this fact, I (8) was able to assign two eye muscles, one in each eye, to each possible canal current, by the following argument.

ASSIGNMENT OF EYE MUSCLES TO CANAL CURRENTS

Endolymph movement being theoretically possible, let us assume that such does occur, bending the cupola and hair cells of a given crista toward or away from the canal to start the stimulus to some or all of the eye muscles which are known to contract in the slow or vestibular component of a nystagmus. If a consistent explanation of all types of rotationally induced nystagmus is obtainable on this basis, the assumption will appear to be amply justified.

It is known that horizontal, rotary and vertical nystagmus, right or left and up or down as the case may be, can be induced in both eyes when only one labyrinth is functioning (9). We may, therefore, approach the problem by studying the phenomena of one labyrinth alone, first when horizontal, then when vertical and finally when rotary nystagmus is being produced.

After rotation to the right with the head 30 degrees forward there should be current in the right horizontal canal from its ampulla. There results horizontal nystagmus with the slow component to the right. This is produced by contraction of the right external and left internal rectus. After rotation to the left, the opposite effect is produced. Thus the crista of the ampulla of the right horizontal canal controls four eye muscles. There has been general agreement as to this. There are two other cristae in the same labyrinth and eight other muscles in the pair of eyes. That each of the remaining (vertical canal) cristae controls four eye muscles is a tempting assumption.

Exact upward movement, starting from the mid-position, is according to Fuchs (10), accomplished only by the combined action of the superior rectus and the inferior oblique. Similarly, downward movement is effected by the inferior rectus and the superior oblique.

Pure rotary movement, with the eye in the mid-position, according to Bárány (11), is performed inward by the superior oblique and superior rectus; outward by the inferior oblique and inferior rectus.

These are the fundamental muscle groups for such movements. When the eyes are voluntarily turned to the right or left, other conditions obtain which will be discussed later.

Consider only the slow or vestibular component of after-nystagmus and that only the right labyrinth is functioning. Incline the patient's head 90 degrees to his right shoulder when seated in the turning chair, rotate him ten times to the right and stop suddenly. This should cause endolymph movement in the *right anterior vertical canal from its ampulla*, and in the right posterior vertical canal toward its ampulla. Vertical nystagmus of both eyes results with the slow component upward. This is accomplished by the *right superior rectus*, the right inferior oblique, the left superior rectus and the *left inferior oblique*.

Next incline the patient's head back 60 degrees from the upright position, rotate him to the right and stop. This should cause endolymph movement in the *right anterior vertical canal from its ampulla* and in the right posterior vertical canal from its ampulla. There results rotary nystagmus with the slow component to the left. This is accomplished by the right superior oblique, the *right superior rectus*, the *left inferior oblique* and the left inferior rectus.

Consider the following proposition: If $X + Y$ causes $A + B + C + D$, and $X + Z$ causes $A + B + E + F$, then X causes $A + B$.

It must be remembered that the above are not equations. They are descriptions of events. If X , Y and Z were push-buttons and A , B , C , D , E and F were electric bells, one would not dispute the conclusion. Use these terms in the foregoing paragraphs which described vertical and rotary nystagmus. The elements common to both have been italicized. One may conclude that X (endolymph movement in the right anterior vertical canal from its ampulla) stimulates A (the right superior rectus) and B (the left inferior oblique).

By similar calculations, and adding the accepted data for the horizontal canals, a list of the effects of each possible canal current is obtained (see tables XIV, XV and XVI). This may be graphically represented as in figure 196.

Using the data in table XVI and figure 196, table XVII was prepared in order to show the details of the fourteen recognized types of nystagmus which can be induced by rotation.

Admitting any endolymph current, the positions and rotations which are listed should affect the canals as indicated by the arrows. The muscles, which according to my analysis are thus stimulated, are

the very muscles needed to produce the types of nystagmus which are known to occur under the conditions specified.

The last two types in table XVII, horizontal with reverse rotary,

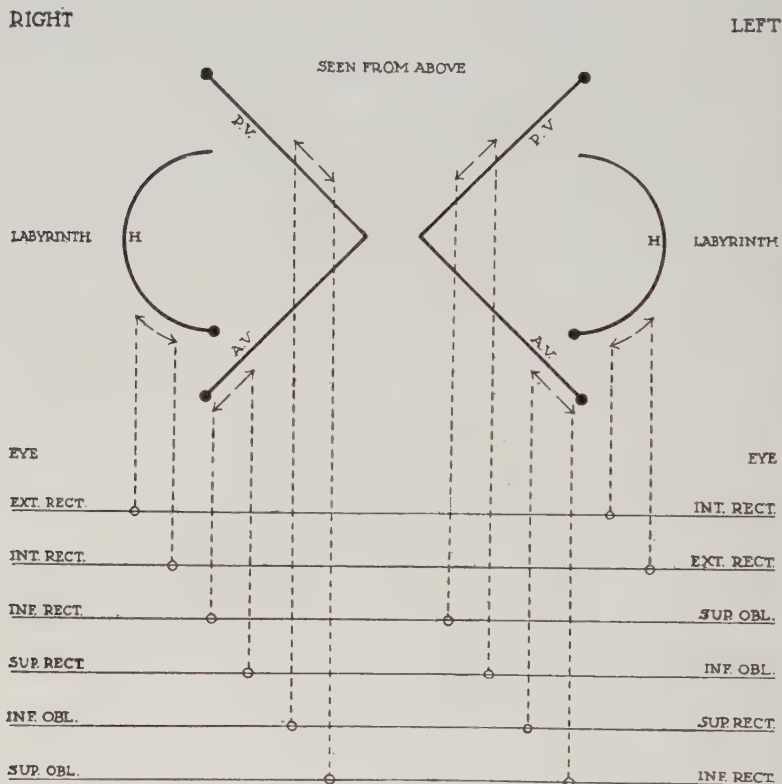


FIG. 196. The relation of individual semicircular canal currents to eye-muscle pairs.

are usually not mentioned in texts on otology. They were predicted by the writer in advance of his producing them but a description of them was subsequently found in Politzer (12).

COMMENT

Ewald's conclusions are adhered to more closely by this assignment than is possible with any other. For example, the response to current in the right anterior vertical canal toward its ampulla is the contraction of the right inferior rectus and the left superior oblique. The nystagmus according to Ewald should be in a plane parallel to the plane of the right anterior vertical canal. This means the right eye must rotate around an axis perpendicular to that plane. Such an axis in man may be imagined as a needle passed horizontally through the right eye-ball center, starting from the posterior lateral surface and emerging on the anterior mesial surface just internal to the cornea, when the eye is in mid-position. The normal action of the right inferior rectus most closely approximates this effect. The same holds good for all the currents and muscle actions.

It was the writer's dissatisfaction with such terms as "reflex response" or "associated movement," which have often been used in discussing induced nystagmus, that led him to attempt a consistent explanation. For certain eye-muscles to contract under given conditions, there must be definite nerve impulses. Every such nerve impulse must have a starting point. While the central pathways are at present unsettled and perhaps will always remain so, the ampullar receptors are definite and varieties of stimuli to one or more cristae can be studied.

Bárány (13) gives rules for determining the form of nystagmus following rotation which involve passing an imaginary plane through the eyeball and parallel to the earth. Movement always takes place in such a plane. For example, with the head erect, the plane will cut horizontally through the eyeball and the nystagmus will be horizontal. With the head 90 degrees to one shoulder the plane will cut through the eyeball in what, were the patient erect, we would call a vertical plane and the nystagmus will be vertical. With the head midway between these two positions the plane will cut obliquely through the eyeball and the nystagmus will be diagonal. At other points between these mentioned the nystagmus will be more or less vertical or horizontal as the case may be. Something more than "reflex" must be offered in explanation of such a complex but well-ordered mechanism. Canal-currents stimulating cristae which function as I have suggested will account for every shade and variety of result. This is most

strikingly emphasized in the case of horizontal with reverse rotary nystagmus.

While in no sense real evidence in favor of the explanation offered, it may be of interest to note the logical uniformity of crista function which this explanation alone presents—namely, each of the two possible bendings of a crista stimulates one muscle in each eye.

There is no doubt that the angles which the planes of the vertical canals make with the sagittal plane vary in individual skulls. It is, however, probable that, if each vertical canal plane makes an angle with the sagittal which is nearer to 45 degrees than to 0 degrees or to 90 degrees, the results of stimulation will be as above described. This would allow a variation between 23 degrees and 67 degrees.

Suppose, however, that we accept the teaching of Ruttin (anterior verticals practically transverse and controlling the oblique muscles, posterior verticals practically sagittal and controlling the superior and inferior recti). In positions used for producing rotary or vertical nystagmus one vertical canal of a given labyrinth will receive the bulk of the stimulus but the other will receive some stimulation. An analysis of the current effects may be made from a consideration of the right labyrinth alone, as follows:

With the head to the right shoulder, rotate to the right and stop. A minor current will run in the right anterior vertical canal from the ampulla. A major current will run in the right posterior vertical canal toward the ampulla. Vertical nystagmus with the slow component upward results. This is produced by the right and left superior recti assisted by the right and left inferior obliques. From the original assumption, then, we find that *current in the right posterior vertical canal toward its ampulla causes contraction of the right superior rectus and left superior rectus.*

Now, with the head 120 degrees forward, rotate to the right and stop. A major current will run in the right anterior vertical canal toward the ampulla. A minor current will run in the right posterior vertical canal toward the ampulla. Rotary nystagmus with the slow component to the right results. This is produced by the right inferior oblique, the right inferior rectus, the left superior oblique and the left superior rectus. From the original assumption, then, we also find that *current in the right posterior vertical canal toward its ampulla causes contraction of the right inferior rectus and left superior rectus.*

This conclusion is inconsistent with the conclusion in the former paragraph. I therefore infer that Ruttin's assignment is incorrect.

A similar analysis on the basis of Lemere's assignment likewise leads to a contradiction.

EXPERIMENTAL PROOF OF THE ASSIGNMENT

A further check on the foregoing assignment of eye-muscles to ampullar stimulation in man was desired. It seemed that the following steps were called for:

1. Obtain a patient with one dead labyrinth.
2. Obtain his consent to ether administration for experimental purposes.
3. Rotate him, when anesthetized, in positions calculated to stimulate only one vertical canal.
4. On stopping the rotation note deviations which will occur in place of nystagmus, since the quick components are abolished by anesthesia.
5. Decide which eye-muscle was responsible for the deviation in each eye.

As the second step of this program was not feasible, some other method of checking was sought.

A study of the canal diagrams shows that there are just twenty-six current pictures possible in each labyrinth. We need to pay attention to the currents of only one labyrinth, as previously explained. Inasmuch as both labyrinths are fixed in the same skull, a canal-current picture produced in one labyrinth by rotation must be accompanied by a certain canal-current picture in the other labyrinth. This second picture is not a duplicate of the first so far as ampullar stimulation is concerned except in positions for producing vertical nystagmus. For example, we cannot by rotation make currents in both horizontal canals toward their ampullae at the same time. When one current goes toward, the other goes away from its ampulla. But, with each of the twenty-six possible current pictures produced in one labyrinth, one of the twenty-six will be produced in the other labyrinth.

Fourteen of these current pictures have already been accounted for in the recognized types of nystagmus. Can the twelve remaining

current pictures with their resulting forms of nystagmus be produced by rotation in the proper positions? Each would call for a current in only one vertical canal of each labyrinth, with or without currents in the horizontal canals.

If one experiments with a glass model of the labyrinth containing some fluid with particles in suspension to show movement, it appears difficult to produce a current in one vertical canal alone. Running upward and inward from their ampullae, the vertical canals of one labyrinth approach each other in perpendicular planes. At their mesial ends they unite in a common crus which then continues to the utriculus. With one vertical canal placed in the horizontal plane, the other vertical canal of this labyrinth will be perpendicular. Rotation now made in the horizontal plane should not produce current in the second canal. But with any slight deviation of the first from the horizontal plane, some stimulus for current production will be present in the second.

When working with a patient this difficulty may be overcome by approaching the ideal position from two opposite extremes and gradually narrowing them down with repeated rotations until the proper position and result is obtained, much as one focuses a microscope.

A second real difficulty lies in the fact that we never know exactly in what planes the canals in a given patient lie. This may be partially met by testing the patient to find at just which head-positions pure horizontal and pure rotary nystagmus may be obtained. Positions for new current combinations may then be calculated with more hope of definite results.

The necessary calculations of position and rotation for the twelve remaining canal-current pictures were made in advance as shown in table XVIII.

These directions for head placement are in a simplified form. For example, the fifth type in table XVIII calls for the head bent 75 degrees forward, then inclined 45 degrees to the right and the patient rotated to the right. This is an abbreviation of the following steps:

First: 120 degrees forward. (Both horizontal canals now perpendicular. Each vertical canal at 45 degrees to the horizontal plane.)

Second: 45 degrees to patient's right. (Both horizontal canals still perpendicular. Right posterior vertical canal and left anterior vertical canal now in

the horizontal plane. Right anterior vertical canal and left posterior vertical canal now perpendicular.)

Third: 45 degrees back. (Both horizontal canals now 45 degrees to the horizontal plane. Right posterior vertical canal and left anterior vertical canal now 45 degrees to the horizontal plane. Right anterior vertical canal and left posterior vertical canal still perpendicular.

120 minus 45 equals 75 which is the total degrees of forward bending required.

The same canal-current picture may also be obtained by: 60 degrees back, 45 degrees left and 45 degrees back with patient rotated to the left. This means that the head must be back an uncomfortable angle of 105 degrees and is hence omitted. Similarly, in each of the remaining types in table XVIII, an alternative but uncomfortable position has been omitted.

The eye-muscles which, according to figure 196, should thus be stimulated were next filled in.

On attempting to produce these effect with careful placement and retention of the head, it was found that there would result, with the eyes in the center position, only a brief nystagmus of two or three jerks after rotation ceased. Furthermore this brief movement was small, indefinite and most difficult of observation or description.

It was then thought that perhaps with voluntary turning of the eyes to the extreme right or left, those expected slow components which arise from the superior and inferior recti and oblique muscles might be more easily observed.

Tables XIX and XX, compiled from data in Fuchs' text-book (14), show that the actions of these muscles are much simpler when the eyes are turned to the right or left.

Using table XIX, I entered in table XVIII the symbols for the slow components to be expected in the twelve instances, first with the eyes to the right and then with the eyes to the left, making twenty-four predictions in all.

Using a patient, in whom I had normally produced all the fourteen recognized types of nystagmus and whose canals were apparently normally placed, I tested him in each of the twelve new positions, first with eyes voluntarily turned to the right after rotation and then with eyes similarly turned to the left.

In all twenty-four tests his nystagmus was exactly as predicted.

TABLE XIV
RIGHT LABYRINTH

POSITION OF PATIENT IN CHAIR AND ROTATION USED	CANAL CURRENT RELATIVE TO AMPULLA	RESULTING SLOW NYSTAGMUS	MUSCLES CAUSING SLOW NYSTAGMUS	CONCLUSIONS
Head on R. shoulder Rot. to R. & stop	A. V. from P. V. to	Vert. Up	Rt. S. R. Rt. I. O. Lt. S. R. Lt. I. O.	Rt. A. V. from stimulates Rt. S. R. Lt. I. O
Head back 60 deg. Rot. to R. & stop	A. V. from P. V. from	Rotary L.	Rt. S. O. Rt. S. R. Lt. I. O. Lt. Inf. R.	
Head on L. shoulder Rot. to L. & stop	A. V. from P. V. to	Vert. Up	Rt. S. R. Rt. I. O. Lt. S. R. Lt. I. O.	Rt. P. V. to stimulates Rt. I. O. Lt. S. R.
Head back 60 deg. Rot. to L. & stop	A. V. to P. V. to	Rotary R.	Rt. I. O. Rt. Inf. R. Lt. S. O. Lt. S. R.	
Head on R. shoulder Rot. to L. & stop	A. V. to P. V. from	Vert. Down	Rt. Inf. R. Rt. S. O. Lt. Inf. R. Lt. S. O.	Rt. P. V. from stimulates Rt. S. O. Lt. Inf. R.
Head for. 120 deg. Rot. to L. & stop	A. V. from P. V. from	Rotary L.	Rt. S. O. Rt. S. R. Lt. I. O. Lt. Inf. R.	
Head on L. shoulder Rot. to R. & stop	A. V. to P. V. from	Vert. Down	Rt. Inf. R. Rt. S. O. Lt. Inf. R. Lt. S. O.	Rt. A. V. to stimulates Rt. Inf. R. Lt. S. O.
Head for. 120 deg. Rot. to R. & stop	A. V. to P. V. to	Rotary R.	Rt. I. O. Rt. Inf. R. Lt. S. O. Lt. S. R.	

TABLE XV
LEFT LABYRINTH

POSITION OF PATIENT IN CHAIR AND ROTATION USED	CANAL CURRENT RELATIVE TO AMPULLA	RESULTING SLOW NYSTAGMUS	MUSCLES CAUSING SLOW NYSTAGMUS	CONCLUSIONS
Head on L. shoulder Rot. to L. & stop	A. V. from P. V. to	Vert. Up	Rt. S. R. Rt. I. O. Lt. S. R. Lt. I. O.	Lt. A. V. from stimulates Rt. I. O. Lt. S. R.
Head back 60 deg. Rot. to L. & stop	A. V. from P. V. from	Rotary R.	Rt. I. O. Rt. Inf. R. Lt. S. O. Lt. S. R.	
Head on R. shoulder Rot. to R. & stop	A. V. from P. V. to	Vert. Up	Rt. S. R. Rt. I. O. Lt. S. R. Lt. I. O.	Lt. P. V. to stimulates Rt. S. R. Lt. I. O.
Head back 60 deg. Rot. to R. & stop	A. V. to P. V. to	Rotary L.	Rt. S. O. Rt. S. R. Lt. I. O. Lt. Inf. R.	
Head on L. shoulder Rot. to R. & stop	A. V. to P. V. from	Vert. Down	Rt. Inf. R. Rt. S. O. Lt. Inf. R. Lt. S. O.	Lt. P. V. from stimulates Rt. Inf. R. Lt. S. O.
Head for. 120 deg. Rot. to R. & stop	A. V. from P. V. from	Rotary R.	Rt. I. O. Rt. Inf. R. Lt. S. O. Lt. S. R.	
Head on R. shoulder Rot. to L. & stop	A. V. to P. V. from	Vert. Down	Rt. Inf. R. Rt. S. O. Lt. Inf. R. Lt. S. O.	Lt. A. V. to stimulates Rt. S. O. Lt. Inf. R.
Head for. 120 deg. Rot. to L. & stop	A. V. to P. V. to	Rotary L.	Rt. S. O. Rt. S. R. Lt. I. O. Lt. Inf. R.	
























TABLE XVI

RECOGNIZED TYPES OF NYSTAGMUS INDUCED BY ROTATION

POSITION OF HEAD	ROTATION	CANAL CURRENTS AFTER ROTATION		EYE MUSCLES STIMULATED		RESULTING SLOW COMPONENT	SYMBOL FOR SLOW	SYMBOL FOR QUICK
		RIGHT	LEFT	RIGHT	LEFT			
30° FORWARD	R	 POSTERIOR SEEN FROM ABOVE ANTERIOR		EXT. RECT.	INT. RECT.	HORIZONTAL TO R.	←	→
30° FORWARD	L			INT. RECT.	EXT. RECT.	HORIZONTAL TO L.	→	←
60° BACK OR 120° FORWARD	R			SUP. OBL.	INF. OBL.	ROTARY OVER TO L.	↶	↷
60° BACK OR 120° FORWARD	L			INF. OBL.	SUP. OBL.	ROTARY OVER TO R.	↷	↶
90° BENT TO R. SHOULDER OR 90° BENT TO L. SHOULDER	R			INF. OBL.	INF. OBL.	VERTICAL UP	↑	↓
90° BENT TO R. SHOULDER OR 90° BENT TO L. SHOULDER	L			SUP. OBL.	SUP. OBL.	VERTICAL DOWN	↓	↑
30° FORWARD AND 45° BENT TO R. SHOULDER	R			INF. OBL.	INF. OBL.	DIAGONAL UP & R.	↗	↘
30° FORWARD AND 45° BENT TO R. SHOULDER	L			SUP. OBL.	SUP. OBL.	DIAGONAL DOWN & L.	↘	↗
30° FORWARD AND 45° BENT TO L. SHOULDER	R			SUP. OBL.	SUP. OBL.	DIAGONAL DOWN & R.	↘	↗
30° FORWARD AND 45° BENT TO L. SHOULDER	L			INF. OBL.	INF. OBL.	DIAGONAL UP & L.	↗	↘
75° FORWARD	R			INF. OBL.	SUP. OBL.	HORIZ. R. & ROTARY R.	↶	↷
75° FORWARD	L			SUP. OBL.	INF. OBL.	HORIZ. L. & ROTARY L.	↷	↶
15° BACK	R			SUP. OBL.	INF. RECT.	HORIZ. R. & ROTARY L.	↶	↷
15° BACK	L			INF. RECT.	SUP. OBL.	HORIZ. L. & ROTARY R.	↷	↶

TABLE XVII

THEORETICALLY POSSIBLE TYPES OF NYSTAGMUS INDUCED BY ROTATION

POSITION OF HEAD	ROTATION	CANAL CURRENTS AFTER ROTATION		EYE MUSCLES STIMULATED		RESULTING SLOW COMPONENT WHEN LOOKING TO			RESULTING QUICK COMPONENT WHEN LOOKING TO		
		RIGHT	LEFT	RIGHT	LEFT	RIGHT	CENTER	LEFT	RIGHT	CENTER	LEFT
60° BACK THEN INCLINE HEAD AS IT IS— 45° RIGHT	R	 POSTERIOR SEEN FROM ABOVE ANTERIOR		SUPRECT.	INF.OBL.	↑		↷	↓		↶
60° BACK THEN, ETC. 45° RIGHT	L			INF.RECT.	SUP.OBL.	↓		↶	↑		↷
60° BACK THEN, ETC. 45° LEFT	R			SUP.OBL.	INF.RECT.	↶		↓	↷		↑
60° BACK THEN, ETC. 45° LEFT	L			INF.OBL.	SUPRECT.	↷		↑	↶		↓
75° FORWARD THEN, ETC. 45° RIGHT	R			INF.OBL.	SUPRECT. EXT.RECT. INT.RECT.	↶		↙	↷		↘
75° FORWARD THEN, ETC. 45° RIGHT	L			SUP.OBL.	INF.RECT. INT.RECT. EXT.RECT.	↷		↓	↶		↑
75° FORWARD THEN, ETC. 45° LEFT	R			INF.RECT.	SUP.OBL. EXT.RECT. INT.RECT.	↶		↷	↑		↶
75° FORWARD THEN, ETC. 45° LEFT	L			SUPRECT.	INF.OBL. INT.RECT. EXT.RECT.	↷		↶	↙		↷
15° BACK THEN, ETC. 45° RIGHT	R			SUPRECT.	INF.OBL. EXT.RECT. INT.RECT.	↶		↷	↓		↷
15° BACK THEN, ETC. 45° RIGHT	L			INF.RECT.	SUP.OBL. INT.RECT. EXT.RECT.	↷		↶	↙		↷
15° BACK THEN, ETC. 45° LEFT	R			SUP.OBL.	INF.RECT. EXT.RECT. INT.RECT.	↶		↙	↷		↙
15° BACK THEN, ETC. 45° LEFT	L			INF.OBL.	SUPRECT. INT.RECT. EXT.RECT.	↷		↑	↶		↓

"RIGHT" OR "LEFT" ALWAYS MEANS THE PATIENT'S.

ARROWS FOR COMPONENTS REPRESENT ACTUAL MOVEMENTS OF PATIENT'S EYES (←=TO RIGHT)

←← OR →→ MEANS HORIZONTAL SLOW COMPONENT IS ABOLISHED BECAUSE EYES ARE VOLUNTARILY TURNED IN ITS DIRECTION.

TABLE XVIII

CANAL CURRENTS RELATIVE TO AMPULLAE	EYE MUSCLES STIMULATED
Rt. A. V. to or Lt. P. V. from	Rt. Inf. R. & Lt. S. O.
Rt. A. V. from or Lt. P. V. to	Rt. S. R. & Lt. I. O.
Rt. P. V. to or Lt. A. V. from	Rt. I. O. & Lt. S. R.
Rt. P. V. from or Lt. A. V. to	Rt. S. O. & Lt. Inf. R.
Rt. Hor. to or Lt. Hor. from	Rt. Int. R. & Lt. Ext. R.
Rt. Hor. from or Lt. Hor. to	Rt. Ext. R. & Lt. Int. R.

TABLE XIX

FUNCTIONS OF INDIVIDUAL EYE MUSCLES IN THREE POSITIONS

MUSCLE	EYES RIGHT	EYES FORWARD	EYES LEFT
Right Sup. Rect.	Elevation	Up-In-Rot. to L.	Rot. to L.
Right Inf. Rect.	Depression	Down-in-Rot. to R.	Rot. to R.
Right Sup. Obl.	Rot. to L.	Down-Out-Rot. to L.	Depression
Right Inf. Obl.	Rot. to R.	Up-Out-Rot. to R.	Elevation
Left Sup. Rect.	Rot. to R.	Up-In-Rot. to R.	Elevation
Left Inf. Rect.	Rot. to L.	Down-In-Rot. to L.	Depression
Left Sup. Obl.	Depression	Down-Out-Rot. to R.	Rot. to R.
Left Inf. Obl.	Elevation	Up-Out-Rot. to L.	Rot. to L.

TABLE XX

EYE MUSCLES WHICH PRODUCE VARIOUS EFFECTS IN THREE POSITIONS

EFFECT	EYES RIGHT		EYES FORWARD		EYES LEFT	
	Right eye	Left eye	Right eye	Left eye	Right eye	Left eye
Elevation	Sup. Rect.	Inf. Obl.	Sup. Rect. Inf. Obl.	Sup. Rect. Inf. Obl.	Inf. Obl.	Sup. Rect.
Depression	Inf. Rect.	Sup. Obl.	Inf. Rect. Sup. Obl.	Inf. Rect. Sup. Obl.	Sup. Obl.	Inf. Rect.
Rot. to R.	Inf. Obl.	Sup. Rect.	Inf. Obl. Inf. Rect.	Sup. Obl. Sup. Rect.	Inf. Rect.	Sup. Obl.
Rot. to L.	Sup. Obl.	Inf. Rect.	Sup. Obl. Sup. Rect.	Inf. Obl. Inf. Rect.	Sup. Rect.	Inf. Obl.

SUMMARY

A possible definite relationship of semicircular canal currents to eye-muscle actions in nystagmus induced by rotation has been considered for years. Certain difficulties in the way of a consistent account are discussed. The author's previously published analysis of the current-muscle relationship is again presented. Reasons are given in favor of this assignment and contradictions in other views are pointed out. The total number of possible currents or combinations of currents in one labyrinth is twenty-six. Fourteen current pictures account for the known types of induced nystagmus. Twelve current pictures remain. Calculations were made as to how to produce these by rotation and what eye-movements would result. Experiment with one normal man showed the results as predicted. The endolymph movement theory and the author's crista-muscle assignment are thus upheld in rotationally induced nystagmus.

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CHAPTER XX

EVALUATION OF CEREBELLAR SYMPTOMATOLOGY ON THE BASIS OF INTRA- AND EXTRA-CEREBELLAR LESIONS¹

MOSES KESCHNER, M.D., AND MORRIS GROSSMAN, M.D.

IT IS generally accepted that the function of the cerebellum is to regulate and coördinate the static and kinetic forces of the organism. Disturbances in this function are at the basis of cerebellar symptomatology. Incoördination or asynergia may, therefore, be said to be the essential symptom of cerebellar disease. As interesting as the various theories of the mechanism of asynergia and its relation to muscle tonus, to deep sensibility, and to ataxia may be, the clinician is primarily interested in asynergia as a sign of cerebellar dysfunction. The other clinical manifestations of cerebellar disease, ataxia, dysmetria, adiodochokinesis, hypotonia, tremor asthenia, and cerebellar catalepsy are merely symptomatic modifications of asynergia.

The conception of the synergic muscular unit as elaborated by Mills and Weisenburg, and later by Lambert and Tilney, has given the clinician insight into the more intimate nature of the anatomic and physiologic factors involved in synergia. A knowledge of these is indispensable to the correct interpretation and evaluation of the symptoms encountered in disease of the cerebellum and the cerebellar pathways.

The object of this communication is an attempt to evaluate the cerebellar symptoms in connection with the other clinical features in 51 cases of intracranial disease verified by operation or autopsy. We regarded cases as "verified by operation" only those in which the operative findings were positive. "Verified by autopsy" refers to macroscopic postmortem findings. We have no available evidence as to what these findings were in serial sections, for purposes of finer localization.

The entire material, clinical as well as pathologic, was collected

¹From the Neurologic Service of the Mount Sinai Hospital in the City of New York.

from the Neurologic, Surgical, Pediatric, and Otologic Services and from the Neuropathologic Laboratory of the Mount Sinai Hospital, from 1920 to 1926 inclusively. It consists of 19 cases of cerebellar neoplasm verified by operation and 8 verified by necropsy; 2 cerebellar abscesses verified by necropsy; 10 of cerebellopontine angle tumors verified by operation and 3 by necropsy; 5 tumors of the brain stem verified by necropsy; 1 tumor of the fourth ventricle verified by operation, and 3 supratentorial tumors verified by necropsy (1 frontal, 1 temporo-parietal, and 1 temporo-occipital).

The first group discussed consists of 29 cases (24 tumors of the lateral lobes, 2 of the vermis and 1 lateral lobe each, 1 of the vermis only, and 2 of cerebellar abscesses). The most common form of *asymrgia* were disturbances in gait. They were found in 27 cases; in most of them the gait was described as "cerebellar," "on a broad base," "staggering," "reeling," or "like that of a drunken man." Most of the patients had a tendency to fall while walking. Seventeen fell to the side of the lesion and 3 to the opposite side; 1 patient fell to the side of the lesion when he first came under observation but later he fell to the opposite side. Two patients had a tendency to fall backward and to the right and left; in 1 of these the lesion was in the vermis and right lobe, and in the other the lesion was in the vermis and left lobe. Another patient fell back and to the right and left; his lesion was in the left lateral lobe. Three patients fell in all directions; in 1 the lesion was in the right lobe, and in the other 2 in the left lobe. It is also noteworthy that 2 patients showed nothing peculiar in their gait except that they advanced the left shoulder while walking; in 1 of these the lesion was in the right lobe, and in the other in the left lobe. Another patient with a lesion in the posteromesial part of the right lobe fell only to the right, and still another who had a trunkal type of gait with falling to the left, showed at necropsy a cyst replacing the entire superior portion of the left cerebellar lobe.

It would seem then that the direction of falling while walking is an important sign in localizing the side of the lesion. This is supported by evidence obtained in experimental and traumatic lesions, limited to the cerebellar lobes. In the usual run of clinical cases, however, the pathologic conditions are not so ideal, and in evaluating this sign it is essential to take into consideration the possible influence of concomitant cortico-spinal involvement on the gait.

Disturbances in attitude of the head were noted in 16 cases. In 10 the occiput was directed to the side of the lesion, and in 6 to the opposite side.

In 15 cases there was falling while in the Romberg position. In 9, the falling was consistently to one side; five of these fell to the side of the lesion, and 4 to the opposite side. The remaining 6 patients fell to either side, but in 2 of these it was more marked to the side of the lesion. One patient with intense vertigo collapsed as soon as he was placed on his feet. Two others who fell while walking, also fell while in the sitting posture, one to the side of the lesion, and the other to the opposite side.

Except perhaps for the position of the head, the attitudes while standing and sitting were not sufficiently constant to be as diagnostic of the side of the lesion as was gait. The special attitudes of the trunk described by some observers were noted in only one of our patients in whom, while in the Romberg position, the trunk was directed to the right and the occiput to the left. The lesion in this case was in the left lateral lobe.

The next most common form of asynergia was cerebellar ataxia; it was present in the upper extremity in 25 cases. The ataxia was unilateral in 20 cases; it was on the side of the lesion in 18, and on the opposite side in 2. In 5 patients it was bilateral, but more marked on the side of the lesion in 4.

Ataxia in the lower extremity was present in 17 cases; it was unilateral in 11; in 9 of which it was on the side of the lesion, and in 2 on the opposite side. It was bilateral in 6, and more marked on the side of the lesion in 5. In 3 cases it was present in all extremities and more marked in the extremities on the side of the lesion. In one of the vermis tumors the ataxia was equally marked in both upper and in one lower extremity; in another case with the lesion in the inferior part of the vermis and in the right lobe, the ataxia was in the right upper extremity and in both lower extremities, but more marked in the left lower; in a third case with the lesion involving the vermis, left lobe, and left middle peduncle, the ataxia was only in the arms and more marked on the left side.

The ataxia was best manifested by a so-called decomposition of movement in the distal parts of the limbs involved. The preponderance of the ataxia on the side of the lesion in the cases in which it is present, makes it an important sign in localizing the side of the lesion.

Adiadochokinesis was noted in 21 cases; it was unilateral in 18, and bilateral in 3; in 15 of the unilateral cases it was on the side of the lesion and in 2 on the opposite side; in one of the vermis cases it was on the left side. In the case where the vermis and right lobe were involved, it was present on both sides, but more marked on the right; in another vermis case where the left lobe and middle peduncle were involved, the adiadochokinesis was present only on the left side. In the bilateral cases it was more marked on the side of the lesion.

It would also seem then that the side of the adiadochokinesis is important in determining the side of the lesion.

Hypotonia was noted in 15 cases. It was unilateral and on the side of the lesion in 5; in 2 it was present in both arms only. In the remaining 8 it was present in all extremities; in 3 of these it was more marked on the side of the lesion.

The hypotonia was associated with hyperactive reflexes in some cases, in others with decreased, and in still others with absent deep reflexes. Likewise no relationship could be established between the hypotonia and the degree of pyramidal tract involvement in cases in which these two conditions coexisted.

Holmes' rebound phenomenon was present in 8 cases. In 5 it was on the side of the lesion; in 2 it was bilateral but more marked on the side of the lesion, while in one case where the lesion was in the vermis it was present only in the left arm. Only 4 cases in which this phenomenon was present showed hypotonia; ataxia however was present in all 8 cases.

Dysmetria was noted in 7 patients. In 4 it was on the side of the lesion, and in 1 on the opposite side. In the remaining 2 it was present on both sides; in 1 of these it was more marked on the side of the lesion, and in the other on the opposite side. Every case in which there was dysmetria, ataxia was also present; in 5 it was also associated with hypotonia.

Tremor was present in 7 patients; 2 had tremor of the head: 1 of these also had tremor of the arm on the side of the lesion. Four others had tremor in both upper extremities, and 1 had tremor in the arm and leg on the side of the lesion. The tremor was coarse and of the type usually designated as cerebellar. In 5 of the cases it was associated with hypotonia.

Cerebellar catalepsy was present in 2 cases; in 1 it was on the side of the lesion, and in the other in all extremities. There was no definite

relationship between cerebellar catalepsy, ataxia, dysmetria, or Holmes' rebound phenomenon.

The occurrence of Holmes' rebound phenomenon, dysmetria, and tremor in relatively so small a number of cases, and their almost constant association with ataxia, would seem to confirm the view generally held that they are merely modifications of asynergia, and, as such, only of corroborative value in the diagnosis of cerebellar lesions.

Spontaneous nystagmus was noted in 23 cases. It was in the horizontal plane in every case, and in 9, also in the vertical plane. The slow component was in as many cases to the side of the lesion as to the opposite side. We could find no discernible relationship between the degree of increased intracranial pressure and the presence of nystagmus, nor could we find any relationship between it and the degree of asynergia. In our opinion this sign needs further investigation before any diagnostic evaluation can be given as to its precise significance in cerebellar disease, especially as regards its usefulness as an aid in indicating the side of the lesion.

Spontaneous past pointing was present in 9 cases. Only 2 of the patients past pointed correctly; in the remaining 7 the direction of the spontaneous past pointing was so inconstant as to be of no localizing value.

The results of caloric examination are recorded in 22 cases. In 2 the examination was unsatisfactory and inconclusive. The results of the tests were in full accord with the neurologic findings in 6 cases. In 2 cases the caloric tests wrongly pointed to a lesion in the lobe opposite to that indicated by the neurologic findings. In 4 the vestibular tests were reported as normal, but the neurologic findings pointed definitely to a lesion in a cerebellar lobe, in which it was found at operation. In 2 cases the neurologic findings pointed to a lesion in the cerebello-pontine angle and the cochlear and vestibular tests confirmed this localization; at operation the lesion was found in each case in a cerebellar lobe and none in the angle. Two patients showed clinical evidences of a posterior fossa lesion; the vestibular tests confirmed the diagnosis of a posterior fossa lesion but shed no further light as to the localization. In one case the signs on admission pointed to a lesion in the left cerebellar lobe; three successive vestibular tests done within one month reported "nothing localizable;" a fourth examination, two months later pointed to a "non-localizable posterior fossa

lesion;" at operation the lesion was found in the left lobe. In another patient the neurologic findings pointed to a tumor in the left cerebellar lobe; the caloric tests confirmed this localization but when the tests were repeated two days later, they were reported as indicating a lesion in both cerebellar lobes; at operation the tumor was found in the left lateral lobe. Finally, in one case the neurologic findings pointed to a lesion in the posterior fossa "side not localizable;" the otologist localized the lesion correctly. (All these tests were done by the otologist to the Hospital.)

The vestibular tests have proved to be important in differentiating labyrinthine from intracranial disease. In some patients with tumors of one or the other cerebellar hemispheres the reactions are sufficiently characteristic to be regarded as confirmatory evidence in localizing the disease; in other patients with intracerebellar disease the results are often ambiguous and afford no aid in establishing a localization, and taken by themselves may even lead to erroneous conclusions.

Involvement of the cranial nerves other than that of the vestibular does not belong to the direct symptomatology of intracerebellar disease. Many cases, however, develop some cranial nerve involvement during some stage of the disease. Many of our cases showed involvement of the third, fourth, and sixth nerves. Very little reliance, however, can be placed on their localizing value.

Papilledema was present in 22 cases. Eight of these showed more marked papilledema on the side of the lesion, and 3 on the opposite side. In 8 the elevation of the discs was equal on both sides; in 2 patients with lesions in the vermis and in 1 lateral lobe, the edema was more marked on the side of the lobe involved in 1, and in the other it was more marked on the opposite side; in another patient with a lesion in the vermis only, the papilledema was equal on both sides. Five patients showed various degrees of post neuritic atrophy prior to operation, and 3 after operation. In 4 cases the papilledema was associated with hemorrhages in the disc. There was a fairly constant relationship between the disc changes and the intracranial pressure.

The trigeminus was involved in 6 cases. In 3, only the sensory divisions were affected; in 2 on the side of the lesion, and in 1 on the opposite side. In 1, both the motor and the sensory divisions were affected on the side of the lesion, and in 1 on the opposite side. In

1 with the lesion in the right lobe the sensory involvement was on the left side, and the motor on the right. In 4 of the cases with trigeminal involvement the intracranial pressure was noted as markedly increased, in 1 moderately increased, and in 1 there was no evidence of increased intracranial pressure.

Diminution or absence of corneal sensibility was noted in 11 cases, in 7 it was bilateral and in 4 unilateral. It was bilateral in 2 of the vermis cases, and unilateral in the third vermis case. Where the involvement was unilateral it was on the side of the lesion in 3, and on the opposite side in 1. In 9 of the 11 cases there was evidence of increased intracranial pressure; in only 2 cases was the disturbance in corneal sensibility associated with involvement of the remaining distribution sensory fifth.

In 24 cases there was faulty innervation of the facial muscles; in 5 of these it was peripheral, and in 19 supranuclear. The peripheral facials were slight and often variable and inconstant; it was on the side of the lesion in 3 and on the opposite side in 2. Supranuclear facial involvement was associated with pyramidal tract involvement in 17 of the 19 cases; in the other 2 it was as inconstant and as variable as in the peripheral cases.

Nerve deafness was present in 5 cases; it was unilateral in 4, and bilateral in 1; in the latter the lesion was in the right cerebellar lobe; in 3 of the former the cochlear involvement was on the side of the lesion; in the fourth the lesion was in the vermis. In 3 cases the nerve deafness was total; in 2 of these the vestibular reactions with the clinical picture was such as to lead to exploration of the cerebello pontine angle and in each case a tumor was found in the cerebellar lobe. Four of the 5 patients with cochlear involvement showed definite increase in intracranial pressure.

The remaining cranial nerves were involved as follows: Three patients had pharyngeal anesthesia and difficulty in swallowing; 2 others showed weakness of the soft palate on the side of the lesion. Of the 3 cases with difficult swallowing 1 occurred in the patient with the lesion in the vermis and right cerebellar lobe. All of these cases showed evidences of marked intracranial pressure.

Speech disturbances, recorded as "cerebellar," "staccato," "scanning" and "explosive" were noted in 5 cases.

Involvement of the pyramidal tracts was found in 24 cases. In 21 the involvement was unilateral, and in 3 it was bilateral; in 1 of these

the lesion was in the vermis and right lobe; in the 21 unilateral cases they were on the side of the cerebellar involvement in 16, and on the opposite side in 5.

Although all of the cases with the pyramidal tract signs, except 1, had evidences of increased intracranial pressure, there was no relationship between the severity of the latter and the intensity of the former.

One case showed total areflexia of the deep and diminution of the superficial reflexes, and 4 showed diminution of all reflexes; in the former the intracranial pressure was unusually increased, and in the latter markedly increased. There were 2 cases with increased intracranial pressure without changes in the reflexes. The changes in the deep reflexes were not always associated with corresponding changes in the superficial reflexes; the same was true as regards to the presence or absence of pathological reflexes.

The daily variability in the reflexes was a striking feature. This was probably due to the periodic variations in the intracranial pressure.

A pendulous knee jerk was noted in 4 cases; in 3 it was unilateral and on the side of the lesion, and in 1 it was bilateral; in the latter the lesion was in the vermis, left lobe, and left middle peduncle. The pendulous knee jerks all occurred in patients with marked hypotonia.

In evaluating these facts we believe we are justified in stating that the great variability in the reflexes minimizes their value as a localizing sign. We feel that by themselves they are not to be taken into consideration in the localization of the intracerebellar lesions. Our cases show that in at least two instances inclusion of the reflex changes in the clinical picture, with a view of being an aid in the localization, led to a wrong interpretation. We feel, therefore, that given a case with signs and symptoms pointing to a lesion in the posterior fossa with all evidences pointing to intracerebellar involvement, the localization of the side of the lesion will depend on the site of the cerebellar signs, and not on the pyramidal tract signs. The presence of pyramidal tract signs and other changes of the reflexes will best be considered as indirect signs and probably indicative of increased intracranial pressure, or extension of the process into neighboring structures.

Mental symptoms were noted in 6 cases; they were similar to those ordinarily encountered in intracranial tumors.

One patient had, before admission, two attacks of rigidity which involved the entire body. We are unable to state whether or not these were "cerebellar fits," another patient had several general convulsions with loss of consciousness before and after operation; and still another had "tonic" and "clonic" convulsions.

Subjective symptoms

There were 20 males and 9 females in the group. Their ages varied between 4 and 55 years. Thirteen were in the first decade of life; of these, 4 patients were 4 years of age; 7 were in the second decade, 2 in the third, 4 in the fourth, and 3 in the fifth decade of life.

The duration of the illness before admission was said to be one month in 1 case, two months in 4 cases, three months in 5 cases, four months in 3 cases, five months in 2 cases, eight months in 1 case, ten months in 1 case, twelve months in 1 case, two years in 1 case, four years in 1 case; in 1 case there was a sudden onset, and in another the date of onset was unknown.

Headache was present in 25 cases; it was the first symptom in 18; it was generalized in 19, frontal in 3, fronto-occipital in 2, and temporo-parietal in 1. Vomiting occurred in 21 cases, and was associated with headache as the first symptom in 12 patients. Vertigo was noted in 13 cases and was the first symptom associated with headache in 4, and it was the only first symptom in 2 patients. Stewart and Holmes state that the vertigo in intracerebellar tumors is usually described as subjective vertigo from the side of the lesion to the healthy side; the transient nature of the vertigo in our cases, with the mental confusion accompanying it associated with the fact that 61 per cent of our patients were individuals in the first decade of life, and the general intelligence of the group was such that we did not consider them sufficiently reliable to permit us to determine in which direction the subjective vertigo was, and therefore we have no reliable data as to this point. General weakness was associated with headache as a first symptom in 3 cases, but all of these patients complained of persistent vomiting. Headache and diplopia were noted as first symptoms in 5 cases. Headache with cyanosis was the first symptom in 1 case. Paresthesias of the face was the first symptom in 2 cases. Disturbance in gait, attitude, and clumsiness associated with headache were the first symptoms in 5 cases. Diminished vision was complained of by 12 patients. Diminished and dimness of vision associated with

headache were the first symptoms in 7 cases. Speech and gait disturbances were the first symptoms in 1 case. Three cases began acutely with fever, headache, and vomiting so that in two the diagnosis of encephalitis was made prior to admission, and in one meningitis was diagnosed. Two patients complained of tinnitus and deafness, and 1 of deafness without tinnitus, before admission. Two others complained of somnolence only.

CEREBELLO-PONTINE ANGLE CASES

Disturbances in gait were present in 8 of the 13 patients in this group. Three walked on a broad base and fell toward the side of the lesion; 1 fell backward and toward the side of the lesion; 1 fell backward and to the right and left, the lesion being on the left side; 1 patient with a bilateral lesion more massive on the left side fell to both sides but more to the left; another patient with the lesion on the right, fell to the right and left, but more to the right, 1 fell to the side opposite to the lesion. In 1 patient with the lesion on the right side gait and station were normal, but she walked advancing the right shoulder.

Disturbances in the attitude of the head were noted in 7 cases; in these the occiput was turned to the side of the lesion in 2; to the side opposite the lesion in 4, and in the case with the bilateral lesions, it was turned to the side of the more massive lesion.

In 7 cases there was swaying and falling in the Romberg position; 4 of these swayed and fell to the side of the lesion; 1 swayed in all directions; 1 to the right and left and forward; and 1 to the right and left and backward.

Twelve of the 13 cases then showed disturbances either in the position of the head, or in gait, or while in the Romberg position. No relationship could be established between the direction of falling, the attitude of the head, and the side of the lesion. It would seem that disturbances in gait are not nearly as valuable in indicating the side of the lesion in cerebello-pontine angle lesions as in intracerebellar lesions.

Eight cases showed ataxia. Four of these had ataxia only in the upper extremities, and 4 others in both the upper and lower. The ataxia in the upper extremities was on the side of the lesion in 6; in the remaining 2 it was bilateral, but more marked on the side of the lesion. In the 4 cases with ataxia in the upper and lower extremities,

the ataxia in the lower was on the same side as that of the upper in 3, and on the opposite side in 1. The patient with the bilateral tumors showed no ataxia.

The ataxia in the cerebello-pontine angle cases was, relatively speaking, less frequent than in the intracerebellar cases, but when present was more marked on the side of the lesion.

Adiadochokinesis was found in 8 cases; it was unilateral in 7, and in 6 of these it was on the side of the lesion; in the patient with the bilateral tumors it was on the side of the more massive lesion; in 1 case it was bilateral but more marked on the side of the lesion. There seems to have been no relationship between the degree of ataxia and adiadochokinesis.

This form of asynergia was, relatively speaking, as frequent as in the intracerebellar cases. Its invariable presence on the side of the lesion gives it importance as a localizing sign.

Hypotonia was not observed in any of the cerebello-pontine angle cases; in one case there was a pendulous knee jerk on the side of the lesion.

Holmes' rebound phenomenon was present in 5 patients, all on the side of the lesion; in 2 it was found in the arm only, and in 3 in the arm and leg.

Dysmetria occurred in 2 cases, also on the side of the lesion.

Three cases had no ataxia, hypotonia, adiadochokinesis or dysmetria.

One patient had a slight tremor of the head, another a tremor of the head and both hands, and a third, an ataxic tremor of the right hand; in this case the lesion was on the right side.

The degree of asynergia in the cerebello-pontine angle cases was never as marked as in the cases of intracerebellar disease.

Spontaneous nystagmus was present in every case. In 9 the slow component was to the side of the lesion, and in 6 of these there was also some nystagmus in the vertical plane; in 4 of the latter there was also a rotatory element to the nystagmus. Two cases had the slow component to the side opposite the lesion; and in 2 others the nystagmus was of the same amplitude in both lateral planes; in 1 of these there was also nystagmus in the vertical plane. In the patient with the bilateral lesions the slow component was to the side of the more massive lesion.

Spontaneous past pointing was noted in 3 cases. In only 1 was the

past pointing correct; in the other 2 the direction of the past pointing was so inconstant that it was impossible to evaluate this sign.

Caloric tests were done in 12 cases; in 10 of these the results of the tests confirmed the clinical diagnosis of cerebello-pontine angle neoplasm. It may perhaps be of interest to note that in only one of these cases was the caloric response typical of a cerebello-pontine angle tumor, and in another patient it was atypical before operation, but became typical one month later. In 1 case the clinical diagnosis was a tumor in the left angle, where it was found at operation, and the otologist reported that the tests indicated a lesion "other than an angle tumor." In another case the caloric tests indicated a lesion in the right cerebellar lobe, and the neurologic findings were those of a tumor in the right angle, where it was found at operation.

In evaluating the results of the caloric tests, we do not hesitate to state that they are considerably more valuable and reliable in localizing cerebello-pontine angle than in intracerebellar lesions.

CRANIAL NERVES

One patient with a tumor in the right angle had loss of the sense of smell on that side and impairment on the other. Four cases showed unequal pupils. The anisocoria bore no relationship to the disc changes. The extraocular muscles were involved as follows: 1 case, with a tumor in the right angle was unable to converge the right eye; 1 patient with a bilateral lesion had insufficiency of both internal recti, and weak upward gaze on the side of the more massive lesion; 1 had involvement of the left superior rectus muscle, the lesion being on the left side. Nine patients showed involvements of the sixth cranial nerve; it was unilateral in 7 and bilateral in 2. In all of the unilateral ones it was on the side of the lesion. Skew deviation was observed in 1 case and, as in 1 of the intracerebellar cases, before operation. there was no definite relationship between the degree of intracranial pressure and the involvement of any of the extraocular muscles, except that in the case with the skew deviation the pressure was enormously increased.

Changes in the fundi were observed in every case. They varied in the different cases from slight blurring of the discs with fullness of the veins, to 5 diopters elevation. The papilledema was equal on both sides in 7; it was greater on one side than on the other in 6; in 4 of these it was greater on the side of the lesion and in 2 on the opposite side.

Three cases showed advanced bilateral post neuritic optic atrophy in addition to papilledema; the atrophy was far advanced on admission. Only 1 case showed minute hemorrhages with the papilledema. The disc changes were in harmony with the degree of increased intracranial pressure.

The trigeminus was affected in 11 cases. In 5 of these there was involvement of both the motor and sensory divisions; in 5 others only the sensory division, and in one only the motor division was involved. In 10 cases the involvement was on the side of the lesion; in 1 with motor involvement only, it was on the side opposite the lesion. In the patient with the bilateral lesions the trigeminus involvement was on the side of the more massive lesion; here the sensory disturbance was only in the lower two branches of the nerve.

Eleven cases showed diminution or absence of corneal sensation; it was unilateral in 8, in 7 of which it was on the side of the lesion; in 3 it was bilateral; 2 of the bilateral cases had the lesion on the left side, and 1 on the right. In 7 unilateral cases the disturbance was on the side of the lesion, and in the patient with the bilateral lesions there was corneal hypesthesia on the side of the more massive lesion.

Facial involvement was noted in 12 cases; in 8 it was peripheral in type, and on the side of the lesion; in the patient with the bilateral lesions it was also peripheral and on the side of the more massive lesion; in another peripheral case it was on the side opposite to the lesion, but in this patient there had been an old suppurative process in the middle ear on that side; in the remaining 2 it was supranuclear and on the same side with the pyramidal tract signs, which were on the side opposite to the lesion; and in 1 it was questionable whether the facial involvement was supranuclear or peripheral, and inasmuch as it was slight and on the opposite side of the lesion no evaluation was given to it. In 8 cases the peripheral facials were quite definite; in 2 others, the involvement was very slight and it was difficult to decide whether it was central or peripheral, but while under observation and with the aid of the electrical tests their peripheral nature became apparent.

Nerve deafness was present in every one of the cases. It was unilateral and on the side of the lesion in 12, and bilateral in 1. It was total in 11 and partial in 2. In the patient with the bilateral tumors it was total on both sides.

The remaining cranial nerves were involved as follows: The soft

palate was paretic on the left side—the side of the lesion in 2 cases; in 1 the uvula deviated to the left (side of the lesion); all 3 cases, however, had pyramidal tract signs on the side of the involvement of the palate and uvula. One patient had difficulty in swallowing, one year before operation; another developed difficulty in swallowing one day after operation; this was associated with a complete palsy of the left side of the larynx and an abductor paralysis of the right side. Two patients had atrophy and fibrillary twitchings of the tongue on the side of the lesion. The patients with pyramidal tract involvement had deviation of the tongue to the side on which the pyramidal tract signs were present. The patient with involvement of the motor and sensory fifth, seventh, and twelfth nerves had drooling of saliva.

Disturbances in speech were noted in 3 cases. These were described as “cerebellar” in 2, and “dysarthric” in 1.

Signs of pyramidal tract involvement were noted in 10 cases; they were marked in 8, and slight in 2; they were unilateral in 8, and bilateral in 2. In these with bilateral signs they were more marked on the side of the tumor; in the cases with unilateral signs, 6 were on the side of the lesion, and 2 on the opposite side. Relatively speaking, pyramidal tract involvement was more frequent in the cerebello-pontine angle cases than in the intracerebellar cases. The periodic variability in the reflexes noted in the intracerebellar group was not observed in the cerebello-pontine angle cases.

Mental changes were noted in 5 cases. One patient had periods of confusion and was irrational on several occasions. Another had apparently had several psychotic episodes during the fifteen years of her illness prior to admission, and became very depressed after operation; another developed a manic state fifteen days after operation, and still another was dull and depressed for months before admission.

Two patients had urinary incontinence; 1 for six months, and the other for five weeks before admission.

Subjective symptoms

There were 6 males and 7 females; their ages (in decades) on admission were as follows: Second decade of life, 1; fourth decade, 4; fifth decade, 6, and sixth decade, 2.

The duration of illness before admission was as follows: Two months, 3 cases; three months, 1 case; six months, 1 case; nine months,

1 case; two years, 2 cases; five years, 1 case; fourteen years, 1 case; fifteen years, 2 cases; twenty years, 1 case.

Headache was present in 10 cases; it was frontal in 4 and generalized in 6. It was the first symptom in 7 cases.

Vomiting occurred in 5 cases and was associated with headache as the first symptom in 2.

Vertigo was present in 9 cases and was associated with headache as the first symptom in 2. In this group, as in the intracerebellar cases, it was impossible to determine the direction of the vertigo. One patient with vertigo as the first symptom never complained of headache.

Diminution of vision occurred in 8 patients before admission; in 2 of these it was the first symptom in association with headache. Four patients complained of diplopia. Paresthesias of the face were present in 6 cases.

Tinnitus was a symptom in 7 cases; in 1 it preceded the deafness by twelve years, and in the other 6 it appeared simultaneously with the deafness.

Deafness was complained of by 11 patients, in 1 of whom it appeared $3\frac{1}{2}$ years before the tinnitus.

General weakness was an early symptom in 2 patients, and weakness in 1 or more extremities in another. Weakness was associated with headache as a first symptom in 2 cases and with vertigo as a first symptom in 1 case.

Disturbances in gait and attitude, and clumsiness were subjective symptoms in 9 patients, before admission.

As a rule, the general symptoms of brain tumor appear earlier and are more pronounced in intracerebellar than in cerebello-pontine angle cases. In the former the cranial nerves are less impaired, and involved later than in the latter. Deafness appears early and is almost invariably present in cerebello-pontine angle tumors. Tinnitus and deafness, associated with involvement of the trigeminus, and of the facial nerve (peripheral) on the same side, are early and almost constant symptoms in cerebello-pontine angle neoplasms. The early onset and greater intensity of the cerebellar symptoms, especially of disturbances in gait, and ataxia is in favor of an intracerebellar lesion. The presence of cerebellar signs on one side, and of pyramidal tract signs on the opposite side, is more in favor of an extracerebellar lesion compressing the pons. The symptoms in

cerebello-pontine angle cases depend a great deal on the size and direction of the growth. In cases in which the tumor begins in the cerebellum the cerebellar symptoms are always more marked than in the cases in which the tumor begins in the angle itself.

BRAIN STEM LESIONS WITH CEREBELLAR SYMPTOMS

This group consists of 6 cases of tumors of the pons and medulla. Five of these were proven by necropsy, and 1, a tumor of the fourth ventricle, by operation. For the purposes of this contribution we have designated this group as the "brain stem group with cerebellar symptoms."

Disturbances in gait were present in 5 patients; it was "cerebellar" in 3, and spastic in 2. One (fourth ventricle tumor) walked holding the head (occiput) to the left, the trunk to the right, and staggered to the left. One had an unsteady gait, walking with the trunk bent forward at the hip with a slight tilt to the left, both legs being set widely apart. One patient staggered to the left. One had a hemiplegic gait and favored the leg on the side of the pyramidal tract signs, and 1 had a spastic gait in the right leg with a tendency to fall to the left.

Disturbances in attitude were noted in 4 cases. Two patients were unable to stand in the Romberg position and fell in all directions. One patient held the head (occiput) to the right, and 1, (fourth ventricle tumor) to the left while walking.

Ataxia was present in 5 cases; it involved all four extremities in 3; in 1 patient, both lower extremities, and in another, the upper and lower extremity on the same side were involved. The patient with the tumor in the fourth ventricle had no ataxia.

Adiadochokinesis was present in 4 cases; it was unilateral in 3 and bilateral in 1.

Hypotonia was present in 3 cases; it was unilateral in 2 and bilateral in another. The patient with the fourth ventricle tumor had hypotonia in both upper extremities only.

Holmes' rebound phenomenon was observed in only 1 case, and it was more marked on one side of the body than on the other.

Two patients had a coarse tremor of the head while at rest, which became more marked on intention. One patient showed an ataxic tremor in the left upper extremity.

The patient with the fourth ventricle tumor showed the following

TABLE XXI
SYMPTOMS AND SIGNS IN INTRA- AND EXTRACEREBELLAR LESIONS

SYMPTOMS			INTRACERE- BELLAR	CEREBELLO- PONTINE ANGLE	BRAIN STEM	SUPRATEN- TORIAL
Cases.....			29	13	6	3
Direct	Asynergia	Gait.....	27	8	3	2
		Head, attitude.....	16	7	2	
		Station.....	15	7	2	1
		Ataxia, upper extremity..	25	8	4	3
		Ataxia, lower extremity...	17	4	5	2
		Adiadochokinesis.....	21	8	4	2
		Hypotonia.....	15		3	1
		Holmes' phenomenon.....	8	5	1	
		Dysmetria.....	7	2		
		Tremor.....	7	3	2	2
		Pendulous knee jerk.....	4	1		
		Cerebellar speech.....	5	2		2
		Cerebellar catalepsy.....	2			
		Cerebellar fits.....	3 ²			
	Vestibular	Nystagmus spontaneous...	23	13	5	1
		Past-pointing spontaneous.	9	3		1
Indirect	Cranial nerves	I.....		1		
		II.....	22	13	5	2
		III-IV-VI.....	11	9	3	3
		Sensory-motor-V.....	6	11	2	
		Corneal-sensibility distur- bance of.....	11	11	4	1
		Supranuclear VI.....	19	2	2	1
		Peripheral VII.....	5	10	3	
		Cochlear VIII.....	5	13	1	1
		IX-X-XI-XII.....	5	5	2	
		Pyramidal-tract-signs.....	24	10	5	3
		Mental symptoms.....	6	5	1	1
	Subjective symptoms	Headache.....	25	10	3	2
		Vomiting.....	21	5	3	2
		Vertigo.....	13	9	2	2
		Vision, diminution of....	12	8	1	
		Diplopia.....	5	4	2	1
		Clumsiness and disturbance of gait and attitude.....	5	9		
		Deafness.....	3	11		
		Tinnitus.....	2	7		
		Paresthesias of face.....	2	6		
		Sphincters, disturbance of.		2		
		Weakness.....	3	2	3	

cerebellar signs: Spontaneous nystagmus, cerebellar gait, cerebellar attitude of the head and trunk, hypotonia of both upper extremities and cerebellar speech.

The cerebellar symptoms in all patients in this group were not as definite as in the preceding groups. This was especially so as regards the ataxia and the adiadochokinesis. The complicating pyramidal tract signs in most of the cases made it difficult to estimate whether the clumsiness was due to asynergia or to pyramidal tract involvement.

Cranial nerve involvement in this group was noted as follows: There was anisocoria in 4 cases. In 1 patient with an extensive

TABLE XXII

SITE OF LESION	CAUSE OF DEATH					TIME OF DEATH		REMARKS
	CASES	Increased intracranial pressure (cases)	Hemorrhage and shock (cases)	Pneumonia (cases)	Meningitis (cases)	First day (cases)	Average number of days after operation	
Cerebellum.....	15	10	4		1	7	2	1 to 2 days after operation
Vermis.....	3	2			1			
Fourth ventricle, pons and medulla..	10	9	1	1		5	5	1 to 18 days after operation
Extracerebellar (including acousticus 12, pontine angle 7, and endothelioma 2).....	21	18	3	3	1	5	4	

pontine lesion both pupils were fixed to light and reacted well to accommodation; he showed neither serologic nor pathologic evidences of syphilis. One patient had a paresis of the superior rectus and an abducens weakness on one side, and another had a weakness of the left internal rectus, and paralysis of both abducentis.

Optic nerve changes were noted in 5 cases. One patient showed, on admission, blurred discs which progressed to 3 diopters swelling within a month, and this was six weeks after the onset of his illness; in this case the cerebrospinal fluid was under normal pressure and there was no evidence of increased intracranial pressure at necropsy.

One patient, whose illness lasted two years, showed no changes in the discs until some weeks before death, when he developed a mild optic neuritis with some pallor of the discs. One patient was admitted with normal nerve heads and within six weeks developed a bilateral papilledema of $2\frac{1}{2}$ diopters; at necropsy the brain showed evidences of marked increased intracranial pressure. One patient showed on admission (one month after the onset of his illness) a bilateral papilledema of 4 diopters; his brain at necropsy also showed evidences of marked increased intracranial pressure. One patient with evidences of marked increased intracranial pressure had normal discs throughout the entire illness which lasted approximately $2\frac{1}{2}$ months. The patient with the fourth ventricle tumor was admitted with a bilateral papilledema of 3 to 4 diopters and beginning optic atrophy, the duration of her illness being six months at the time of admission.

The fifth motor cranial nerve was involved in 2 cases; it was unilateral in both. The sensory division of the fifth was intact in all 6 cases.

Disturbances in corneal sensibility were noted in 4 cases; it was bilateral in 3 and unilateral in 1.

Disturbances in facial innervation were noted in 5 cases; peripheral in 3, and supranuclear in 2, in association with pyramidal tract signs; the supranuclear involvement was in one case on the side of the pyramidal tract signs, and in the other case with evidences of bilateral pyramidal tract involvement it was on the side of the more marked pyramidal tract signs.

Cochlear involvement (unilateral) was noted in one case.

Spontaneous nystagmus was noted in 5 cases; in 4 it was present in both horizontal planes, and in 2 of these it was also vertical and oblique; in the case with the fourth ventricle tumor, spontaneous nystagmus was noted only on looking to the right.

None of the patients in this group pass-pointed spontaneously.

Caloric tests were performed in 4 cases. They were unsatisfactory in the patient with the fourth ventricle tumor; in another case no definite conclusions could be drawn; in the remaining two, the tests corroborated the clinical diagnosis of a stem lesion.

Difficulty in swallowing and dysarthria were noted in one case. Another had involvement of the ninth and tenth cranial nerves on one side, and of the eleventh and twelfth (peripheral) on both sides.

Pyramidal tract signs were present in 5 cases (in all patients except

in the one with the fourth ventricle tumor); they were bilateral in 3, and unilateral in 2. None of the cases showed a clear cut "paralysis alternans." One patient had mental symptoms, euphoria and emotional instability.

Subjective symptoms

There were 3 males and 3 females in this group. Four patients were in the first decade of life, 1 in the third, and 1 in the fourth. The youngest patient was three, and the oldest thirty-nine years of age. In one case no history of the mode of onset could be obtained. In the remaining 5, 3 had generalized headache and 2 others had vertigo; 3 complained of weakness of the extremities; 2 had persistent vomiting; 2 complained of double vision and another of poor vision. A note-worthy feature in this group was the relatively early appearance of the general symptoms of brain tumor.

A review of the histories and clinical signs of the cases in this group, in the light of the postmortem findings permits of no definite conclusions. Some of the outstanding features may be said to be: The predominance and earlier appearance of the pyramidal tract and cranial nerve signs over the cerebellar signs. The asynergia is, as a rule, less definite in quality and situation. The cranial nerve symptoms are often bilateral and more general in the brain stem cases than in the intracerebellar and cerebello-pontine angle cases. Our pathologic and clinical data in this small group of cases give us no clues as to what one is to expect clinically from involvement of any of the cerebellar peduncles. The nature of the cerebellar symptoms, in the light of our personal experience and from what we could gather from the literature, cannot be utilized as a diagnostic factor in an attempt to postulate with any reasonable degree of certainty the localization of lesions in the peduncles. The diagnosis must be made, not on the nature and distribution of the cerebellar symptoms but on their association with other symptoms due to involvement of the pons and medulla, and on the history and chronologic appearance of each symptom.

THE SUPRATENTORIAL GROUP OF CASES WITH CEREBELLAR SYMPTOMS

To illustrate the difficulties encountered clinically in evaluating cerebellar symptoms in cases of intracranial neoplasms we will cite, in more or less detail, the following cases:

Case 1. A forty-year old man was admitted to the Hospital with a history of attacks of vertigo, loss of memory and emotional instability of three years' duration. On examination he showed sluggish pupils, a left hemiparesis and a bilateral low grade optic atrophy, a cerebellar tremor, ataxia and adiadochokinesis in both upper extremities more marked in the left, hypotonia on the left side and a monotonous staccato speech. His frontal region was explored and no neoplasm was found. Necropsy showed an endothelioma 2 inches in diameter involving the dura in the mid-line between the inferior surface of both frontal lobes compressing the olfactory tracts; the tumor infiltrated the right frontal lobe and impressed itself into the left frontal lobe; it had penetrated for about $1\frac{1}{2}$ inches into each frontal lobe; the corpus callosum was not involved; the ventricles were small and not disturbed. Another tumor 1 cm. in diameter was found upon the dura overlying the anterior part of the petrous portion of the left temporal bone; it had also penetrated through the dura.

Case 2. A sixteen-year old girl was admitted to the Hospital complaining of vertigo and nausea for five months after which she developed diplopia, slowness of speech, a staggering gait with paresthesias of the right side of the body. During this period she had one convulsion (generalized) after which she was semicomatose for three days. Two weeks before admission she noticed difficulty in hearing and one week later she had an olfactory hallucination. She had lost 10 pounds during the month prior to her admission. Examination revealed normal fundi, a complete right hemiparesis with bilateral ankle clonus, right pupil larger than left, some vertical nystagmus, right homonymous hemianopsia, skew deviation, bilateral corneal hypesthesia, definite bilateral ataxia and adiadochokinesis more marked on the right, falling to the right while walking, and a positive Romberg. The spinal fluid came out under increased pressure. Ventriculography showed obliteration of the left lateral ventricle and a dislocation of the right lateral and third ventricles. Operation revealed a large infiltrating glioma in the left cerebral hemisphere. The tumor presented itself on the surface in two places: (1) between the frontal and parietal lobes posteriorly to Broca's area, and (2) beneath the surface pushing up the brain in the occipital lobe at the supramarginal terraces; it was not removable.

Case 3. A forty-one-year old man was admitted to the Hospital with an "acute" history of three days' duration, of vertigo, excruciating headache and pain in the occipital region, rigidity of the neck, tremor of the hands and persistent projectile vomiting. On admission his pulse was 60, temperature 100°F., and he was in semi-stupor. Examination revealed the left pupil larger than the right, normal fundi, slight bilateral external rectus weakness, slight right supranuclear facial weakness, hyperreflexia on the right side with marked rigidity of the neck and a bilateral Kernig. Lumbar puncture yielded a bloody spinal fluid under moderate pressure. His condition remained stationary for two days after which he was suddenly seized with a "tonic" fit associated with loss of consciousness; during the fit his entire body assumed a typical decerebrate rigidity; during the next two days he had three similar seizures. Following the last seizure his gait became ataxic and he developed marked asynergia in all four extremities, horizontal and vertical nystagmus and a coarse head tremor. The vestibular tests were reported as indicating an intracerebellar lesion. He remained in this condi-

tion for six weeks when he gradually began to improve; after two more weeks he had practically recovered except for some slight ataxia in the upper and lower extremities. He was quite comfortable for the next two months when his headache and vertigo recurred and his ataxic gait became more marked. Examination at this time revealed the left pupil larger than the right, early bilateral papilledema, left homonymous hemianopsia, left astereognosis and disturbances in postural sensibility in the limbs on the left side, and a left hemiparesis with an equivocal plantar response on both sides. The cerebellar signs were not as definite as at the onset of the illness. His spinal fluid was clear, under moderate pressure and contained 24 lymphocytes. His general condition became progressively worse and he died about five months after the onset of his illness. At necropsy the brain showed evidences of increased intracranial pressure. A tumor (spongioblastoma) 7 by 4 cm. was found on the inferior surface of the right temporo-occipital lobes; it lay posteriorly to the thalamus and mesially to the optic radiation; it had broken through to the surface, on the mesial side of the right occipital lobe dislodging the mesencephalon of the opposite side and compressed the brain stem in the region of the quadrigeminal plate; the aqueduct of Sylvius was reduced to an oblique slit. The tumor also invaded the posterior horn of the left lateral ventricle part of which was collapsed.

The occurrence of cerebellar symptoms in other supratentorial lesions than those illustrated by the cases above described (frontal, suprasellar, temporal, etc.) is too well known to necessitate comment. Neurologic literature is teeming with descriptions of various criteria for the differentiation of so-called frontal lobe ataxia, temporal lobe ataxia, rubral ataxia, hyperkinesia, etc., from the ataxia due to disease of the cerebellum itself. We have not been successful in making such differentiation at the bedside from the nature of the cerebellar symptoms, and are, therefore, unable to confirm or to deny the tenability of the various differential criteria. As a matter of fact, the three cases cited in detail and selected at random from the available clinical material illustrate the exception to the well established rule that cerebellar symptoms in supratentorial lesions appear late, whereas those in posterior fossa lesions are usually present from the onset of the illness. In every one of these three cases the clinical picture began with cerebellar symptoms and signs. A correct evaluation of cerebellar symptoms produced by lesions in localizations other than those of the cerebellum itself, from the history and clinical findings may frequently be almost impossible. It is in such cases that encephalography is of the greatest aid in reaching a diagnosis.

DISCUSSION

The following questions submitted to Dr. Keschner before the Commission, together with the answers to them, are here reported verbatim.

DR. WILLIAM G. SPILLER: Has any attention been paid in this study to the sign that Oppenheim described, *viz.*, the loss of the conjunctival reflex in tumors of the posterior cranial fossa, and if so, was there any relation of the site of the tumor to the side on which the loss of the conjunctival reflex occurred?

To what degree have changes been found in the sella turcica by x-ray examination, as a result of tumors of the cerebellum or of the cerebello-pontile angle?

DR. MOSES KESCHNER: Our intracerebellar cases showed diminished or absent corneal sensibility in 11 patients. The corneal involvement was bilateral in 7 and unilateral in 4. In the unilateral cases it was on the side of the lesion in 3 and on the opposite side in 1. Nine of the 11 cases presented evidences of increased intracranial pressure. In only 2 cases was it associated with involvement of other branches of the sensory division of the trigeminus.

As to the second question: The cases that showed roentgenographic changes in the sella turcica all presented clinical evidences of markedly increased intracranial pressure. The cases that showed no evidences of increased intracranial pressure presented no x-ray change in the appearance or size of the sella, and the clinoid processes appeared normal.

DR. ADOLF MEYER: To what extent have you had an opportunity in these cases to study the postoperative findings and to compare them with the preoperative findings in cases in which definite parts of the cerebellum were removed?

DR. KESCHNER: We did not think that this phase of the problem came within the scope of our paper and I am, therefore, unable to present any such data.

DR. WEINBERG: Did you find any difference in the direction of the vertigo, both of the patient and the external world, in the intra- and extra-cerebellar lesions?

DR. KESCHNER: As far as we have been able to gather, Stewart and Holmes were probably the first to point out that when a patient has an intracerebellar lesion external objects seemed to move in the direction opposite to the lesion, and at the same time the patient's body seemed to go in a similar direction; whereas if the lesion is extracerebellar external objects seemed to move in the direction opposite to the lesion but the patient's body would seem to go to the side of the lesion. With this in mind, we paid special attention in our study to the direction of the vertigo. Unfortunately most of our patients were so sick with dizziness and vomiting that it was absolutely impossible to reach any definite conclusions or to enable us on the direction of the vertigo to make any differentiation as to whether the lesions were intra- or extracerebellar.

Section V

TREATMENT

CHAPTER XXI

SURGICAL TREATMENT AND POSTOPERATIVE PROGNOSIS OF CEREBELLAR TUMORS

ALFRED W. ADSON, M.D., AND HARRY L. PARKER, M.D.

THIS review includes our experience in the treatment of 215 patients with lesions in the posterior fossa affecting the cerebellum. In 12 of these tumor was suspected but the lesion was found at necropsy or operation to be inflammatory. There were thus 203 cases of tumor. Each lesion is discussed separately, the clinical syndrome described, with emphasis on the diagnostic features, and the surgical considerations and results presented. The literature, the microscopic pathology and the results of radiotherapy are not discussed.

ANESTHESIA

In the early group of our cases, anesthesia was induced by the intratracheal administration of ether; later it was administered intrapharyngeally and, since 1920, by simple inhalation. During the last three years we have employed local anesthesia with paravertebral anesthesia of the upper six cervical nerves in perhaps more than half of the cases. On employing the cerebellar headrest, which we introduced and described in 1919, we learned that it was unnecessary to administer the ether intratracheally or intrapharyngeally, since this headrest permits normal breathing during the anesthetic. The headrest is so arranged that the head is held firmly, and can be raised, lowered, or tilted without interfering with respiration. The mouth and nose extend through the frame without pressure on the respiratory passages and, if mucus collects, it drains from the mouth readily. An ether mask is suspended under the headrest; it is easily removable and permits the entrance of sufficient air at all times.

Local anesthesia has a decided advantage over general anesthesia. It diminishes bleeding, eliminates the unpleasant effects which follow a general anesthetic, and permits the surgeon to follow the condition of the patient much more closely. It is contraindicated in extremely nervous and emotional patients, and in young children. If the symp-

toms do not indicate pressure on the medulla, preoperative medication of morphine and atropine may be administered before the operation. However, morphine embarrasses respiration and can be used only in a limited number of cases of cerebellar disease.

During operation, the blood pressure is measured every five minutes by the anesthetist. This is of distinct value, since a drop in blood pressure can be observed before a disturbance in pulse can be detected; it thus serves as a warning to the surgeon to interrupt the operation or resort to transfusion.

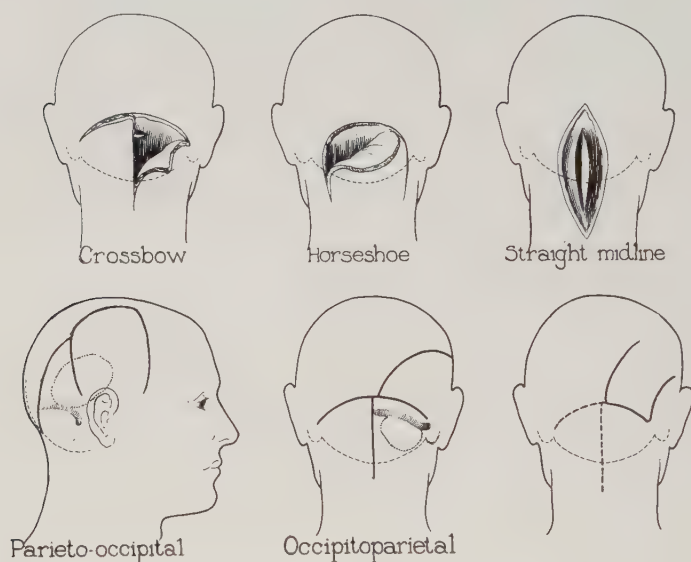


FIG. 197. Various incisions employed in exploration of the posterior fossa

INCISIONS

The Cushing cross-bow and median-line incision (fig. 197) is usually employed, since it permits ample exposure of the cerebellar lobes, the cerebello-pontine angle, and the medulla. A flap is reflected on each side over each cerebellar hemisphere and the cerebellum exposed widely on each side. The skin and muscle flaps are made at different levels, to permit more accurate closure of the muscle flap, the fascia, the galea, and the skin.

The horse-shoe flap employed by Elsberg is satisfactory in thin-

necked patients, but otherwise fails to provide sufficient exposure. It consists of a single flap only, and, since it is not divided in the center as is the Cushing cross-bow incision, exposure of the cerebello-pontine angle is more difficult.

The median-line incision suggested by Sachs can be employed satisfactorily in children if extensive operation or exploration of the angle is not anticipated. It has the advantage of requiring less time for making and closing and can be converted into a cross-bow incision when necessary. The occipital flap, in conjunction with the cross-bow cerebellar flap, suggested by Naffziger, is of advantage occasionally in exposing tumors at the angle. We have employed a combined occipito-cross-bow incision for tumors arising from the angle, the tentorium, and the lateral sinus. This incision consists of the cross-bow incision and exposure of the cerebellum with reflection of the osteoplastic occipital flap forward and laterally; all of the bone from over the lateral sinus and the occipital lobe is reflected, and sufficient space provided for ligation of the lateral sinus and resection of it with the tumor. In low-lying tumors of the occipital lobe we employ a parieto-occipital osteoplastic flap in conjunction with a cerebellar flap, which is reflected posteriorly and laterally, again uncovering the lateral sinus and the upper and lateral aspects of the cerebellar lobe; this permits resection of the tentorium and of the lateral sinus, when the tumor is adherent.

VENTRICULOGRAPHY

Ventriculography is of diagnostic value, especially in children, in differentiating a median-line tumor and communicating hydrocephalus. However, it should not be employed when the history and the clinical data are sufficient to determine the site of the lesion.

In our series of 215 patients, ventriculography was used in 18. In 13 it was of diagnostic or confirmatory value, in 3 it was valueless, and in 2 it proved misleading. In 12 of these 18 cases the diagnosis was verified: at operation in 6, and at autopsy in 6. In 4, death occurred between the time of ventriculogram and cerebellar exploration, ranging from one to five days following ventriculographic examination. Three patients died suddenly after forty-eight hours, the course following ventriculographic examination in all having been apparently as it was before. All 3 died while being raised from a reclining to sitting position, just prior to partaking of food. Technically these

deaths might not have been charged to ventriculography, but rather to intracranial pressure produced by marked internal hydrocephalus; further, had the patient been explored a few hours after the ventriculogram was taken, death would have been charged to exploration rather than to ventriculography. It is obvious that the ventricles fill rapidly after ventriculographic examination and removal of air, and that repeated drainage of the ventricle is necessary if exploration is to be postponed a few days.

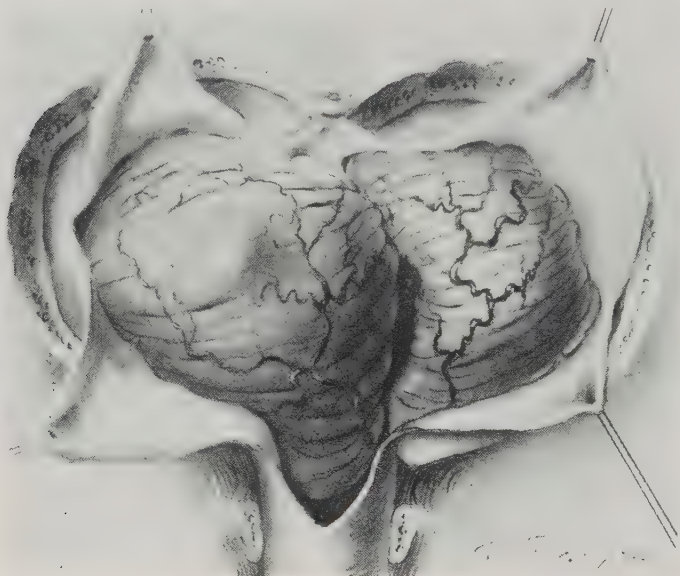


FIG. 198. Surgical illustration of unilateral enlargement of a cerebellar hemisphere with prolapse of the lobe through the foramen, due to subcortical tumor of the cerebellar hemisphere.

TUMORS OF THE CEREBELLAR HEMISPHERES

Tumors producing cerebellar symptoms may be cortical or subcortical, solid or cystic in type, or they may be extracerebellar, compressing the cerebellum. The symptoms of these intracerebellar tumors are homolateral ataxia, dyssynergia, dysmetria, dysdiadochokinesia, and atony of the muscles of the limbs on the involved side with diminution in reflexes. Nystagmus, vertigo, and tilting of the

head are present when the vestibular nuclei are compressed. If the tumor is slow in growth, the localizing signs may antedate the symptoms of intracranial pressure.

To explore cerebellar tumor, the skin and muscle flaps are reflected and the cerebellum is exposed bilaterally over a wide area. Since the



FIG. 199. Horizontal section of the cerebellum, illustrating a cystic glioma

cerebellar hemisphere is frequently prolapsed through the foramen magnum (fig. 198), it is well to include, in the cerebellar exposure, removal of the dorsal portion of the foramen magnum and dorsal portion of the arch of the atlas. When the dura is under tension, the posterior horn of the lateral ventricle should be aspirated to prevent

herniation of the brain and rupture of the blood vessels on incision of the dura. The dura should be opened widely, the occipital sinus ligated and divided, and the dural incision extended down over the medulla and upper cervical cord. Unless it is necessary to explore the medulla and the fourth ventricle, the arachnoid should not be opened. After having determined the site of the tumor by its appearance, by the unilateral enlargement of the cerebellar hemisphere with prolapse through the foramen magnum, or by the widened and flattened cerebellar convolutions, the surgeon endeavors to determine the size and character of the lesion. Meningiomas are obvious, but infiltrating tumors may be entirely subcortical or may extend to the surface. Cystic tumors (fig. 199) can be recognized by their fluctuation and, on aspiration with a brain cannula, yield a clear, yellow, syrupy fluid which clots readily on standing. Before the cyst is exposed and completely emptied, it is well to ligate the cortical vessels and incise the cerebellar hemisphere parallel to the cerebellar convolutions. With proper illumination, the cavity of the cystic tumor can be explored; usually a nodule will be found in the wall of the capsule, which should be removed, if possible. The cystic wall should likewise be removed, if possible, or fixed with Zenker's solution, which is applied to the walls of the cyst with pledgets of cotton. Special care should be taken to prevent the Zenker's fluid from extending to the surface of the brain or running down around the medulla. After the pledgets have remained in contact with the cystic wall for five minutes, the cavity should be irrigated thoroughly with normal solution of sodium chloride, care being again exercised to avoid any contact of the solution with the normal brain. The cyst should be allowed to remain open, and the wound should be closed in the usual manner.

Solid subcortical infiltrating tumors differ from cystic degenerating gliomas only in their lack of fluctuation; they give the impression of firmness, slightly greater than that of the cerebellar hemisphere. A brain cannula, graduated in millimeters, may be inserted to ascertain the depth of the tumor and the degree of resistance. Unless the tumor is deep in the brain, it should be explored after ligation of the cortical vessels and incision of the cortex, as in exploration of a cystic tumor. Biopsy should be carried out whenever possible to verify the diagnosis. Grossly, subcortical tumors are regarded as gliomas, and are classified clinically in three groups: cystic tumors, soft cellular vascular tumors,

and nonencapsulated, slowly growing, infiltrating, fibrous tumors. With the aid of Del Hortega and Cajal stains they may be divided into: spongioblastomas, neuroblastomas, medulloblastomas, astrocytomas, and so forth, depending on the particular cell involved.

If a glioma is definitely circumscribed, an attempt at removal may be justifiable; if it is large and is producing marked pressure, resection of a portion of it may be justifiable, but if it is extensive and infiltrating

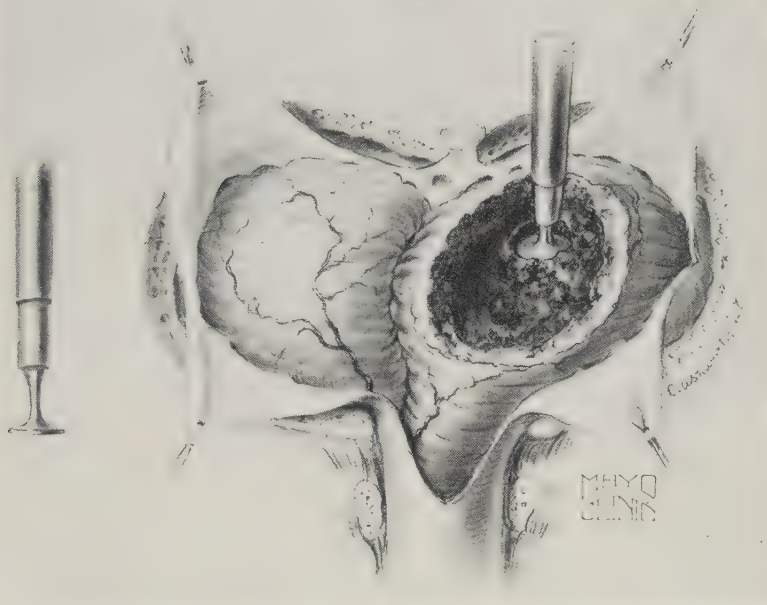


FIG. 200. Partial removal of an infiltrating glioma of the right cerebellar hemisphere by surgical diathermy.

in type, little is to be accomplished except for the decompression. Radiotherapy or surgical diathermy (fig. 200) may be employed as palliative measures.

A review of our series shows that cystic gliomas occur more frequently in children, while solid tumors are more common in adult life. Occasionally, one may find a simple cyst, containing yellow, gelatinous, syrupy fluid, without any gliomatous nodule; the cyst may be of embryonic origin or result from vascular disturbance. We have

observed several cases in which a pseudocyst developed between the muscle flap and the arachnoid covering the cerebellar hemisphere subsequent to operation. This, we believe, arose from failure of the cerebrospinal fluid to take its normal course underneath the arachnoid. While it is true that the basilar cistern remains undisturbed, there is less likelihood that fluid will accumulate between the muscles and the arachnoid over the cerebellar hemispheres if the arachnoid over the cistern is not torn. Occasionally it is necessary to open the arachnoid for exploration of the vermis and the fourth ventricle, but then one is compelled to choose between the effects of pressure from some obstructing lesion and the effects of a postoperative pseudocerebellar cyst.

It is essential, in treating inoperable tumors of the cerebellum, to perform wide bilateral cerebellar decompression and to leave the dura wide open before closing the wound. The muscle plane should be closed with interrupted silk sutures, the fascia covering the muscle should be closed separately with similar sutures, the galea and skin by layers of silk. Unless care is taken in closing the muscles and the fascial layers, disfiguring herniation will result. We prefer to treat inoperable gliomas and recurrent tumors by irradiation rather than radically, except in cases of recurrent cystic tumors.

TUMORS OF THE VERMIS

Tumors involving the vermis may be situated either in the anterior or the posterior portion, and usually occur in children under the age of twelve, most frequently in those under the age of six. The symptoms are abrupt in onset, and are of short duration. Marked intracranial pressure occurs with headache, vomiting, severe choking of the discs, and stiff neck. The localizing symptoms consist of marked ataxia, equal on both sides, and usually affecting the lower extremities and the trunk more than the upper extremities, so that there is a great tendency to pitch forward or backward. Frequently, the neck is rigid, and the head retracted; palsy of the external recti and diplopia, together with paralysis of the conjugate lateral movements of the eyes, are common manifestations. Other localizing signs are absent, as a rule, until the tumor produces pressure on the floor of the fourth ventricle with medullary herniation, when death may occur abruptly. Pathologically, tumors of the vermis are either gliomas or spongiomedullo-blastomas.

Recognition of a vermian lesion is often difficult, inasmuch as the symptoms are not unlike those arising from hydrocephalus. While it is true that there is a congenital obstructive hydrocephalus, not infrequently obstructive hydrocephalus may develop as the result of ependymitis with occlusion of the aqueduct subsequent to a contagious disease as measles, whooping-cough or scarlet fever. Communicating hydrocephalus may arise from similar causes, but its course is more protracted; it is due to changes in the arachnoid and villi, and the failure of the cerebro-spinal fluid to be absorbed as rapidly as it should be. Circumscribed cystic arachnoiditis and occlusion of the fourth ventricle from adhesions between the cerebellar hemispheres and vermis and medulla may arise from similar causes and produce symptoms similar to those of a vermian tumor. In making a differential diagnosis, one must consider carefully the history of onset. In vermian tumors, the onset of symptoms is abrupt; in hydrocephalus, unless congenital, the onset of symptoms is less abrupt and is preceded by a contagious disease or perhaps some other acute infection. Ventriculographic examination may be advisable before exploration, to determine the site of the block which may be in the aqueduct, in the fourth ventricle or its foramina, or in the posterior cistern. Occasionally, puncture of the cistern may be employed to demonstrate communicating hydrocephalus, but at all times such procedures should be performed in the operating room where the surgeon is prepared to go on to cerebellar exploration, should signs of respiratory embarrassment develop.

Another differentiating factor which should be given consideration is the degree of choked disc, which in tumors of the vermis quickly becomes extreme (from 3 to 7 diopters). In hydrocephalus the choked disc progresses slowly and rarely attains an elevation of more than 3 diopters in the obstructive type and rarely more than 1 or 2 diopters in the communicating type. These data are not absolute, but serve as a fairly reliable guide.

The median-line incision may be employed in the exploration of vermian tumors, but if the exposure is found insufficient, it should be converted into a cross-bow incision. Again, bilateral decompression should be performed, and the cerebrospinal fluid should be aspirated from the posterior horn of the lateral ventricle to relieve the tension prior to incision of the dura.

Tumors of the vermis are similar in appearance to those of the

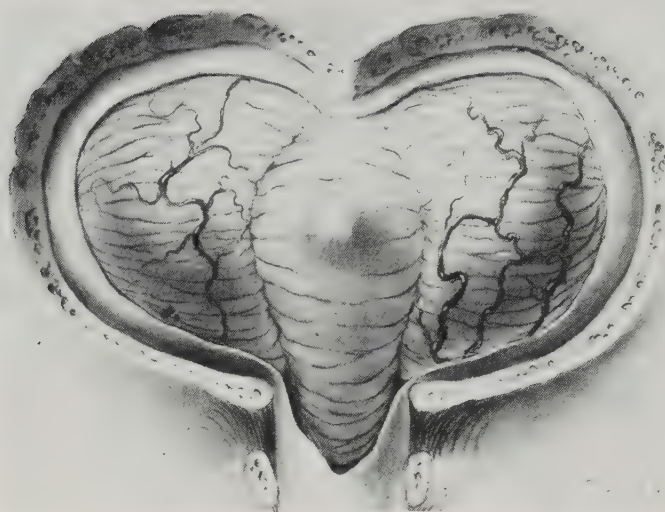


FIG. 201. Surgical illustration of a tumor in the posterior portion of the vermis with marked prolapse through the foramen magnum.

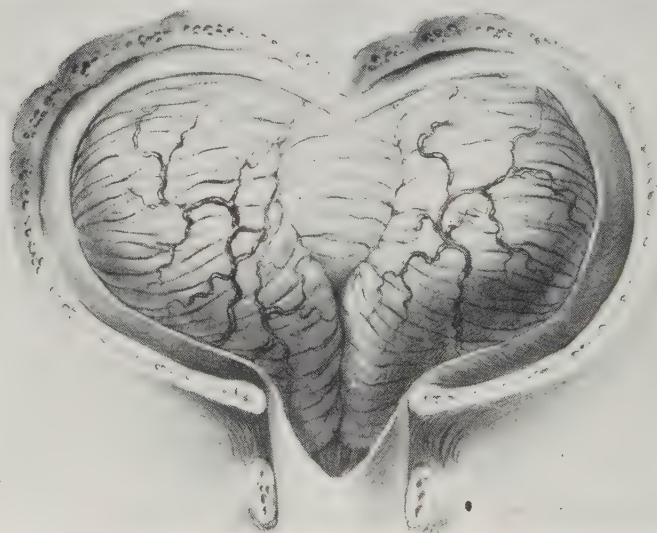


FIG. 202. Surgical illustration of a tumor in the anterior portion of the vermis

cerebellar hemisphere, and produce flattening and widening of the convolutions of the vermis with prolapse of the vermis through the foramen magnum (fig. 201); if the anterior portion of the vermis is involved, equal tongue-like projections develop from both cerebellar hemispheres which prolapse through the foramen magnum (fig. 202). The tumor may be confined strictly to the vermis, or it may invade one or both cerebellar hemispheres. Cystic tumors fluctuate and are easily recognizable by the bluish membrane which is present on the surface. Solid tumors are similar in appearance to those found in the cerebellar hemispheres (fig. 203).

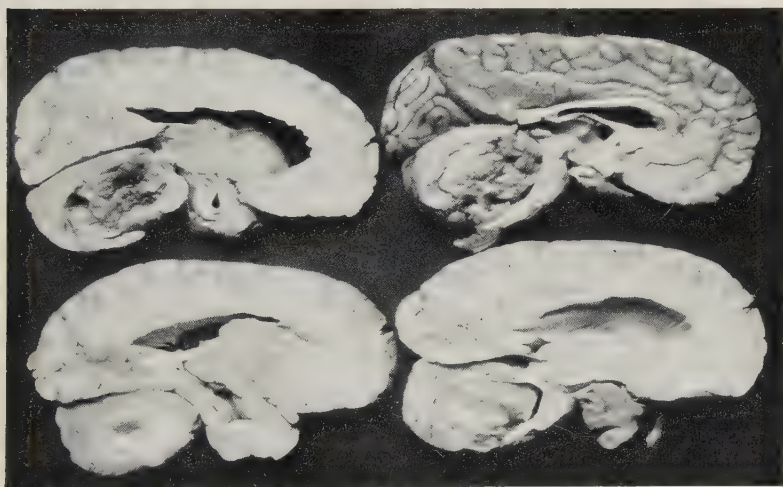


FIG. 203. Sagittal sections illustrating a tumor of the vermis

They are treated in the same way as tumors of the cerebellar hemisphere, except that one is more frequently justified in resecting the lower part of the vermis and splitting the anterior portion longitudinally in order to relieve the pressure over the fourth ventricle. Decompression and closure are carried out as in tumors of the cerebellar hemispheres; postoperative treatment is the same as in all tumors of the brain operated on.

TUMORS OF THE CEREBELLAR PEDUNCLES

Tumors originating in cerebellar peduncles usually involve the cerebellar nuclei and cortex sooner or later, either by direct invasion

or by the effects of pressure. The symptoms are similar in onset, progress, and development to those of tumor of the cerebellum proper. Symptoms due to its influence on neighboring structures are usually more marked than are those of lesions of the hemispheres and vermis.

The surgical approach is similar to that employed for cerebellar tumors, except that tumors of the cerebellar peduncles are less accessible and the surgeon must frequently resort to bilateral cerebellar decompression instead of attempting any type of removal. Post-operative treatment is carried out as in lesions of the cerebellum proper.

GRANULOMAS

Tuberculoma of the cerebellar hemispheres and vermis occurs occasionally but is rarely recognized as such, unless an increase in lymphocytes and bacilli of tuberculosis are found in the spinal fluid. As a rule, tuberculomas are nodular, and readily recognized by their firmness and the presence of small, bead-like nodules on the surface or along a vessel supplying the mass. If the identity of a tuberculoma is determined, surgical treatment is contraindicated, since the course of life is limited. If a tuberculoma is found accidentally, having been diagnosed cerebellar tumor, the surgeon has the option of allowing it to remain undisturbed or removing it. If an attempt is made to remove it, the vessels should be ligated with silk before the tumor is excised. In the series of patients observed at the Mayo Clinic, only one cerebellar tuberculoma was encountered; the immediate surgical convalescence was uneventful, but death occurred several weeks later from tuberculous meningitis. One of us (Adson) has removed four isolated tuberculomas of the cerebrum; one of the patients died shortly after operation, the other three recovered from the operation but lived only a few months. It is questionable whether much is accomplished by surgical intervention in tuberculoma of the brain. Occasionally, one may encounter a syphiloma of the cerebellum, which is usually recognized by the clinical history and the positive serologic examination; syphiloma of the cerebellum is not amenable to surgical treatment and should be treated by antisyphilitic methods. Occasionally, too, echinococcus cysts develop in the cerebellum; however, we have encountered neither a syphiloma or an echinococcus cyst in our series.

EXTRACEREBELLAR TUMORS

Extracerebellar tumors include acoustic tumors, tumors of the cerebellopontine angle, meningiomas, tumors of the floor of the fourth ventricle, pons and medulla, and spinocerebellar tumors.

Acoustic tumors

Acoustic tumors or the so-called neurofibroma of the eighth nerve may occur as isolated tumors, are rarely bilateral, but may be associated with a general neurofibromatosis. The local symptoms usually antedate those of intracranial pressure; the characteristic history is an early complaint of tinnitus on the affected side, which may continue for months before deafness develops. The deafness, like the tinnitus, progresses gradually until complete, when the tinnitus is lost, and the cochlear and vestibular functions of the eighth nerve are completely abolished. This process may continue from a few months to several years before other symptoms develop. Then paresis of the face slowly develops, with occasional paroxysmal spasms of the facial muscle as the tumor increases in size, followed by diplopia with weakness of the external rectus, pain, and paresthesia over the distribution of the second division of the fifth nerve. Motor weakness of the muscles supplied by the third branch with loss of the corneal reflex on the affected side soon follows. Nystagmus, vertigo and ataxia or atony of the arm and leg on the affected side result from pressure on the cerebellum and its tracts. Dysphagia and aphonia occur when the ninth and tenth nerves become involved. Failure of response to caloric stimulation of the affected side is confirmatory evidence of involvement of the eighth nerve. Tilting of the head and rigidity of the neck usually take place when symptoms of intracranial pressure become manifest. The general symptoms of headache, choked disc, and vomiting appear when the lesion has grown to such size as to interfere with the outflow of cerebrospinal fluid and produces internal hydrocephalus.

Acoustic tumors vary considerably in size, depending on the duration of growth. They are usually rounded or oval, and frequently produce erosion of the petrous bone in the region of the internal auditory meatus. They may grow directly toward the median line, indenting and displacing the pons dorsally and to the opposite side, or they may extend mesially and upward or mesially and downward

toward the foramen magnum. If the growth of the tumor is of short duration, it presents a pinkish nodule within the eighth nerve, with little or no evidence of pressure on the pons or cerebellum; this type may be resected in toto. The tendency for the patient with tinnitus is to continue to consult otologists until cerebellar signs have become manifest, when the tumor has developed to such size that indentation with displacement of the pons and cerebellar hemisphere has occurred. The tumor may increase to between 5 and 7 cm. in its long axis; generally, it presents areas of fatty degeneration and a yellow, patchy appearance. It is always encapsulated, and only occasionally cystic. The lateral portion or the capsule is free from adhesions and blood vessels, as a rule, but the dorsal and mesial surfaces are invariably adherent to the cerebellum and pons, are covered with branches from the cerebellar artery and veins, and are difficult to dissect free from the surrounding structures; attempt to dissect usually provokes serious complications. For this reason, we prefer to use the intracapsular enucleation suggested by Cushing, which consists of thorough exposure of the tumor after elevation and displacement of the cerebellar hemisphere; the use of cotton strips is advisable to protect the cerebellum during the surgical manipulation. An illuminated retractor gives sufficient and satisfactory illumination during operation.

The usual cerebellar method of approach is followed. A linear or crucial incision is made over the lateral aspect of the tumor, and the contents of the growth are removed from within the capsule by a brain-scoop or curet. Since much of the tissue in large acoustic tumors has undergone fatty degeneration, this procedure results in fairly complete removal. Occasionally, undegenerated glial or fibrous elements predominate, in which event intracapsular removal is less successful (fig. 204) and radium therapy is indicated. Acoustic tumors rarely occur in children. Generally they occur in early or middle life; at times, also, after middle life. The latter group of patients are poor surgical subjects, as a rule, and it is in this group as well as in the group in which extensive acoustic tumors produce marked indentation and displacement of the pons that surgical fatality is prone to occur. Rather than subject the patient to extensive eradication or intracapsular enucleation, we have used radium needles in three instances during the last year (fig. 205). Five 10 mgm. radium needles were inserted at equidistant points into the tumor and allowed to remain in place for from eighteen to twenty-four hours. The

results following the administration of radium and cerebellar decompression are probably not as good as those obtained by intracapsular

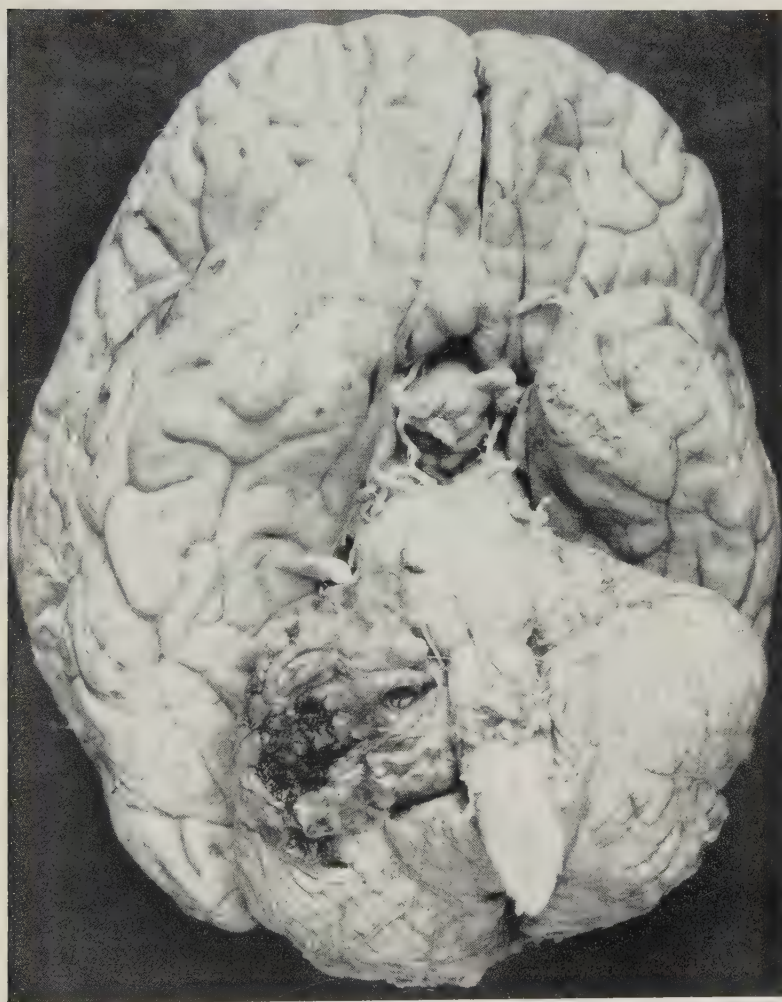


FIG. 204. Ventral view of an acoustic tumor, partial intracapsular removal of which had been performed.

removal, but the surgical risk in these extreme cases is decidedly less and moderate relief is afforded.

Bilateral cerebellar decompression, without surgical interference with the tumor and without radium emanation, frequently relieves the symptoms of intracranial pressure for an appreciable time. This is illustrated in one of our cases: the patient was completely relieved of headache, vomiting and papilledema, has been able to carry on his work as a miller for seven years and is still working. The use of radium with decompression should afford additional relief and should permit many of these patients to live out their life expectancy in moderate comfort.

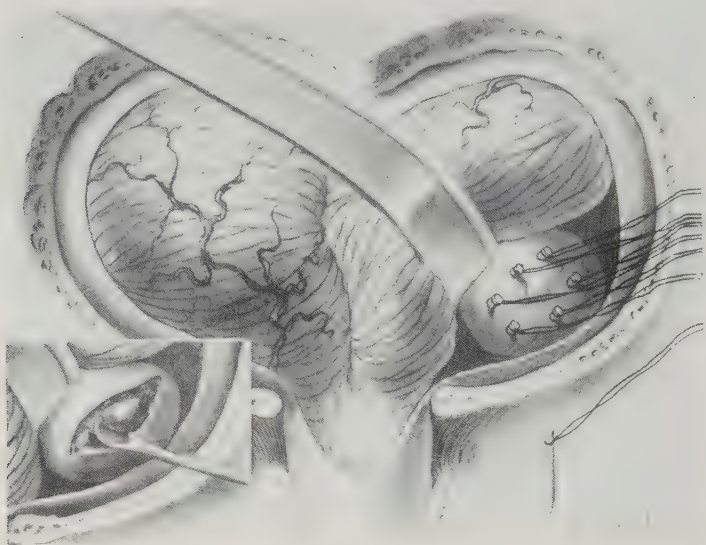


FIG. 205. Surgical illustration of an acoustic tumor, showing the two procedures usually employed: intracapsular enucleation and radium needles inserted at equidistant points into the mass.

The closure of the wounds incidental to operations on acoustic tumors is similar to that for cerebellar tumors.

Tumors of the cerebellopontine angle

Tumors of the cerebellopontine angle may arise from the meninges as endotheliomas, or from the blood vessels as hemangioma-endotheliomas and sarcomas, or they may arise from the parenchyma of the

cerebellum, the cerebellar peduncles or the pons as gliomas, or neuroblastomas. They vary in size, depending on the nature of the

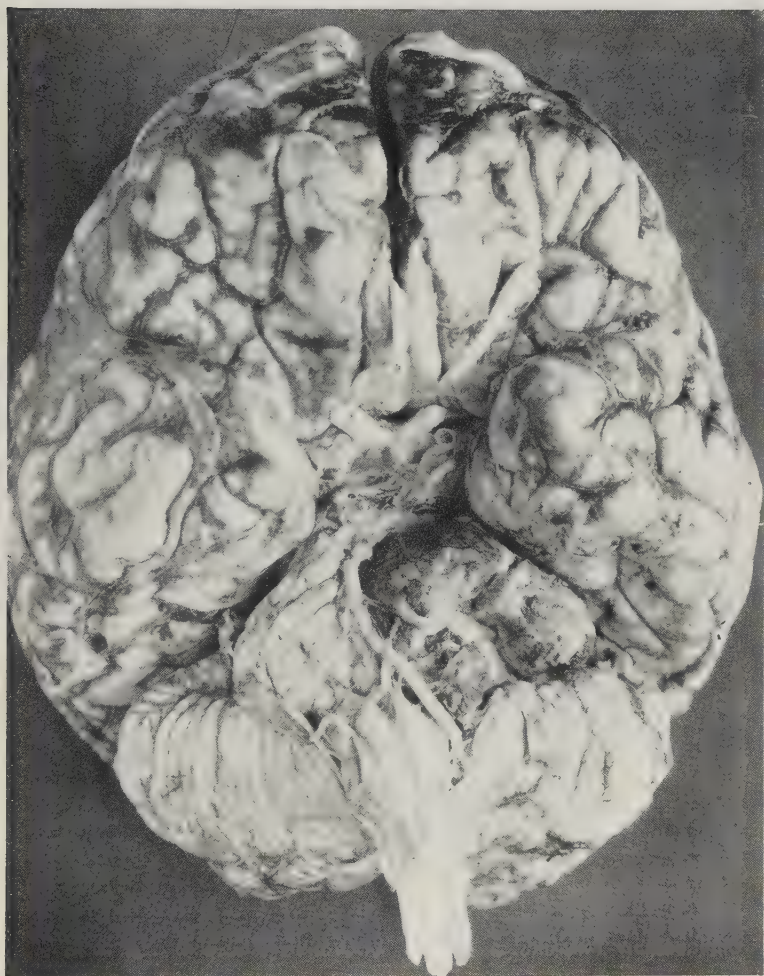


FIG. 206. Ventral view of a tumor of the cerebellopontine angle, producing marked compression and displacement of the pons, medulla, and cerebellum.

tumor and the duration of growth (fig. 206). They are frequently covered with bands of adhesions and with veins or branches from the

cerebellar artery. Infiltrating tumors of the pons or cerebellum extending into the angle may cause similar displacement but more often they destroy and infiltrate the tissues. Such cases are inoperable, although some of the encapsulated tumors of the angle are operable.

The clinical syndrome associated with tumors of the cerebellopontine angle consists of progressive involvement of the fifth, sixth, eighth, ninth, tenth, eleventh, and twelfth cranial nerves on the affected side, usually in the order named, with varying degrees of severity. The eighth nerve is affected simultaneously with or later than the other nerves; this permits differentiation of tumor of the angle from a true acoustic tumor. In tumors of the cerebellopontine angle, the fifth cranial nerve is involved early, at times to the extent of producing complete anesthesia over its distribution with paralysis of the masticatory muscles. The cerebellar symptoms, as ataxia, nystagmus and vertigo, occur as the tumor grows and encroaches on the cerebellum. The signs of increased intracranial pressure, headache, vomiting, and papilledema, appear much earlier in tumors of the cerebellopontine angle than they do in acoustic tumors and are usually more acute and more rapidly progressive. Their surgical consideration is open for discussion. Some neurologic surgeons affirm that all localized brain tumors should be explored, others assert the contrary.

The surgical approach is similar to that employed for acoustic tumors; if the tumor is found to be inoperable, radium needles in conjunction with bilateral cerebellar decompression is the best procedure. The results so obtained are not nearly as satisfactory, unfortunately, as those obtained by similar treatment of acoustic tumors. If a tumor of the cerebellopontine angle is found to be a meningioma, removal may be possible; if the exposure afforded primarily is found to be insufficient, a secondary operation may be undertaken, with an additional occipital flap, to provide sufficient exposure for extirpation. If the surgeon is ultra-conservative, he may rightly feel justified in refusing to operate when the history is short and the symptoms marked, in view of the marked surgical hazard and the slight degree of benefit to be expected from operative treatment. In cases of this kind, it is well to inform the patient, or the patient's relatives, of the gravity of operative treatment and the questionable nature of the results.

MENINGIOMAS OF THE POSTERIOR FOSSA

Meningiomas of the posterior fossa have no specific clinical syndrome, except that the symptoms may be of long duration. Since these tumors may be situated anywhere in the posterior fossa, arising from the arachnoid and becoming adherent to the dura, or lying over the cerebellar hemisphere, the vermis, or the medulla (fig. 207), in the cerebellopontine angle or from the tentorium cerebelli, or the lateral

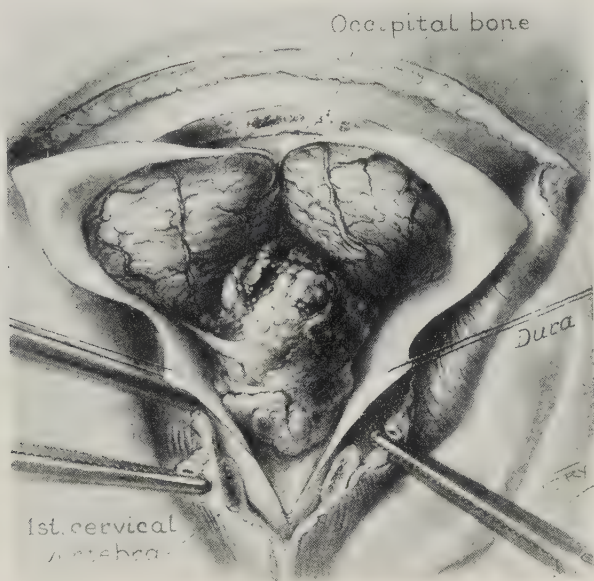


FIG. 207. Surgical illustration of a meningioma situated at the margin of the foramen magnum with an extension through the foramen, compressing the medulla and upper cervical cord.

sinus, a variety of clinical phenomena should be expected, depending directly on the areas of brain affected. The surgical approach, again, is a cross-bow and median-line incision with bilateral cerebellar decompression. If the procedure is associated with a great deal of bleeding and the exposure is insufficient, a second-stage operation may be necessary. The results are most satisfactory if removal has been completed without injury to the brain or interference with its

blood supply. The usual closure and the usual postoperative treatment, without irradiation, are employed.

TUMORS OF THE FOURTH VENTRICLE

Tumors arising from the floor of the fourth ventricle are usually ependymomas or subependymal gliomas; those arising from the choroid plexus are frequently papillomas; those arising from the roof of the fourth ventricle (vermis) are gliomas and spongioblastomas. The clinical syndrome is similar to that of vermial tumors: sudden,



FIG. 208. Sagittal section of a pedunculated tumor of the fourth ventricle

acute, marked internal hydrocephalus with truncal ataxia, diplopia, rigidity of the neck, and retraction of the head. Vomiting is an early and incessant symptom, and may occur prior to the appearance of headache. Hiccough occurs frequently and is a pronounced symptom. The periodicity of symptoms in pedunculated tumors is a characteristic phenomenon; that is, sudden onset of severe headache, vomiting, papilledema, slow pulse, and coma with just as sudden recovery. Postural influence is of diagnostic value; sudden increase in symptoms occurs on change of posture and death may occur suddenly and unexpectedly.

The surgical considerations are similar to those of vermial tumors. The usual bilateral cerebellar decompression and exploration is employed with the same precaution to prevent herniation and rupture of the vermis and cerebellar hemispheres. Tumors of the fourth ventricle invariably cause widening and flattening of the convolutions of the vermis and, in order to expose the tumor, it is necessary to split the vermis longitudinally and retract both cerebellar hemispheres. If the tumor is a papilloma or is pedunculated (fig. 208), complete removal with satisfactory result may be hoped for. However, not infrequently the tumor is infiltrating in character and inoperable, and all that can be accomplished is cerebellar decompression.

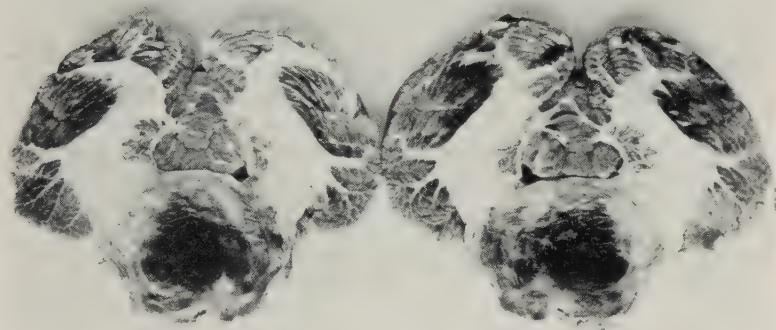


FIG. 209. Section of the cerebellum, vermis and pons, illustrating a bilateral infiltrating tumor of the pons.

sion or perhaps a splitting of the tumor with partial removal in an attempt to relieve the obstruction of the aqueduct and the fourth ventricle. Radicotherapy should be considered in the latter cases. Closure and postoperative management are carried out as for cerebellar tumors.

PONTINE AND MEDULLARY TUMORS

Pontine and medullary tumors (figs. 209 and 210) are of the infiltrating type and are gliomas, medulloblastomas, spongioblastomas or, occasionally, tuberculomas. The characteristic clinical syndrome is homolateral involvement of the fifth, sixth, and seventh cranial

nerves with heterolateral hemiplegia; the signs of intracranial pressure are late in appearance, and ataxia and nystagmus are associated symptoms. Since pontine tumors often affect both sides of the pons, the symptoms are usually bilateral. Weakness of the lateral conjugate movements of the eye is common, due to bilateral involvement of the posterior longitudinal bundle.

Tumors of the medulla produce similar symptoms with less likely involvement of the fifth, sixth, and seventh nerves and bilateral

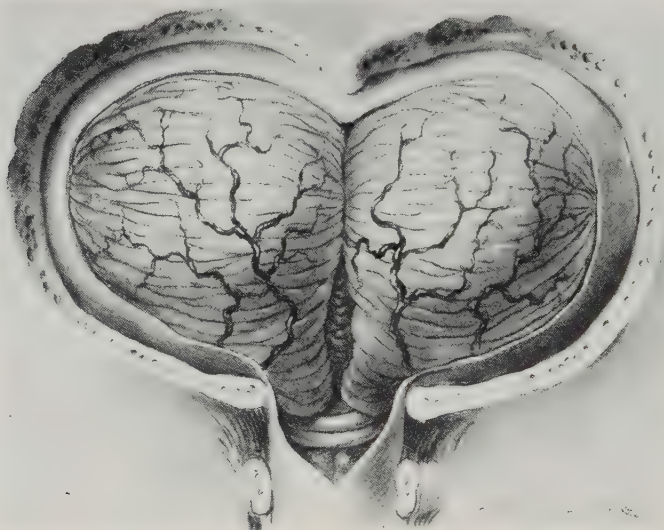


FIG. 210. Surgical illustration of a tumor of the medulla, producing lengthening of the medulla with rugae on the dorsal surface.

involvement of the ninth, tenth, eleventh, and twelfth nerves. Signs of intracranial pressure are late in appearance, and hemiplegia and quadriplegia develop alternately, according to the relative position and size of the tumor. Cerebellar symptoms occur according to the degree of involvement of the adjacent cerebellar lobes and tracts.

The surgical treatment is limited to cerebellar decompression, which may offer temporary relief. However, in the majority of cases, sufficient relief is not afforded to warrant cerebellar exploration and decompression, since localizing symptoms usually manifest themselves

before signs of intracranial pressure develop; these are the only symptoms that are relieved by cerebellar decompression.



FIG. 211. Surgical illustration of a cerebellospinal tumor

TUMORS IN THE REGION OF THE FORAMEN MAGNUM

These tumors may be primarily spinal and extend through the foramen magnum into the posterior fossa, or the reverse, but in either

instance combined laminectomy and cerebellar exploration is necessary (fig. 211). If the tumor is of spinal origin, it will be found to correspond to lesions of the spinal cord. It may be an extradural tumor, a neurofibroma of the first or second cervical root, a hemangio-endothelioma, or a subdural extramedullary tumor, as fibroma, neurofibroma, or hemangio-endothelioma; it may be a glioma of the cord, extending into the medulla. If the tumor originates in the posterior fossa, it will usually be found to be a meningioma (fig. 207) or a neurofibroma.

The symptoms produced by cerebellospinal tumors have some features in common with those found in tumors of the cord, with early root pain in the occipital nerves; if the tumor is intramedullary, however, no pain is present and compression symptoms slowly progress producing the classical Brown-Sequard syndrome. As the tumor grows, bilateral symptoms occur with more complete compression of the cord: sensory and motor paralysis develops to a high level, the reflexes are exaggerated below the level, and there is sensory loss in the distribution of the occipital nerve and weakness of the sternocleidomastoid and trapezius muscles. Cerebellar symptoms develop only when the tumor extends sufficiently into the posterior fossa to produce pressure on the cerebellum. Symptoms of increased intracranial pressure appear only occasionally; they are caused by obstruction to the outflow of cerebrospinal fluid. Rigidity of the neck with abnormal postures of the head is a characteristic symptom.

For exploratory purposes, a median-line incision over the upper cervical vertebrae and the occipital area is used. After the muscles are retracted, laminectomy is performed in conjunction with cerebellar decompression. If the tumor is subdural, the dura is opened over the cervical cord, and the incision is extended far enough upward in the median-line to expose the tumor. The dissection must necessarily be gentle, and special precautions must be taken against injuring the vertebral arteries. One vertebral artery can be ligated without complications. It is not uncommon to find the phrenic nerves and the nerves supplying the accessory muscles of respiration involved, in which event extreme care must be taken in manipulating the cord and the medulla to avoid injury and instant death from respiratory failure. The surgical hazard can be reduced further by the employment of paravertebral anesthesia instead of ether anesthesia; ether acts as a pulmonary irritant, and anything that can be done to reduce

the strain on the respiratory system is of distinct advantage. Many of these patients already have difficulty in obtaining sufficient air. It is often necessary to divide the operation into two stages: the first stage consists of laminectomy and a cerebellar decompression, with an incision into the dura; removal of the tumor constitutes the second stage.

In the series studied, we included one meningioma which originated on the inner margin of the foramen magnum, extended down through the foramen magnum and compressed the upper cervical cord, but we did not include tumors of the upper part of the cervical cord. Intramedullary tumors usually extend from the medulla into the upper cervical cord and are difficult to treat; decompression affords little relief.

REVIEW OF CASES

This review includes a series of 215 cases, in which we performed 237 operations. In 144 cases there were infiltrating lesions of the cerebellar hemispheres, vermis, fourth ventricle, pons, brain stem, and medulla, and in 71, noninfiltrating, encapsulated extracerebellar lesions. A two-stage operation was performed in 12 cases, and a three-stage operation in 5.

In the group of 144 infiltrating neoplasms, 93 of the patients were males, 51 females; the oldest was seventy-three, the youngest two years. The average age in this series of patients was twenty-three years. Thirty-nine patients were below the age of twelve. The identity of the tumor was verified in 103 either at operation or necropsy; they were found in the following situations:

Cerebellum.....	61
Vermis.....	13
Fourth ventricle.....	14
Brain stem.....	6
Medulla.....	5
Pons.....	4
Infiltrating tumors which were subcortical but unverified by pathologic studies.....	41

In the group of 71 extracerebellar, noninfiltrating, encapsulated lesions, 46 of the patients were males and 25 were females. The oldest was sixty-four, the youngest thirteen; the average age in this

series was thirty-nine. The following lesions were verified, either at operation or at necropsy:

Acoustic tumors.....	37
Tumors of the cerebellopontine angle.....	19 (4 endotheliomas)
Endotheliomas in the posterior fossa but not in the angle.....	3
Cerebellar tumor suspects which proved to be communicating hydrocephalus due to arachnoiditis.....	12

The pathologic report on the tissue removed in the total series of 215 cases was as follows:

Neurofibroma.....	37
Glioma (solid, degenerating, and cystic).....	43
Tuberculoma.....	1
Endothelioma.....	8
Psammoma.....	1
Fibroma.....	1
Sarcoma.....	6
Spongioblastoma.....	4
Neurocytoma.....	1

There were 51 deaths, a surgical mortality of 21 per cent. The operative mortality varied considerably for the various intracerebellar and extracerebellar tumors; it was lowest in cystic gliomas and in cerebellar tumors, and highest in tumors of the fourth ventricle, pons, and medulla. The mortality has been reduced decidedly during the last three years, by the substitution of local anesthesia for ether anesthesia; this not only minimizes the danger of respiratory embarrassment but also aids in the control of hemorrhage.

In attempting to ascertain the causes of death in this series, we have investigated the site of the tumor, the length of the interval between operation and death, and the probable contributory factors (see table XXII).

It will be noted that the chief cause of death, where the tumor was inoperable, was increased intracranial pressure. This may be combated in a small number, perhaps, by intravenous administration of hypertonic solutions. The effects of hemorrhage may be controlled by careful hemostasis and transfusions, and by operating in two or three stages. Elevation of temperature on the second and third days after operation is often due to an increase in intracranial pressure, which may be reduced, at times, by the use of ventricular puncture, or by spinal puncture if the block has been removed.

DIFFERENTIAL DIAGNOSIS

There are certain conditions which may symptomatically simulate tumors of the cerebellum or its peduncles; among these must be considered supratentorial tumors, as well as inflammation and degeneration affecting the cerebellum or its tracts. Among such supratentorial tumors, those involving the midbrain and the structures around the third ventricle and the frontal lobe provide the chief sources of

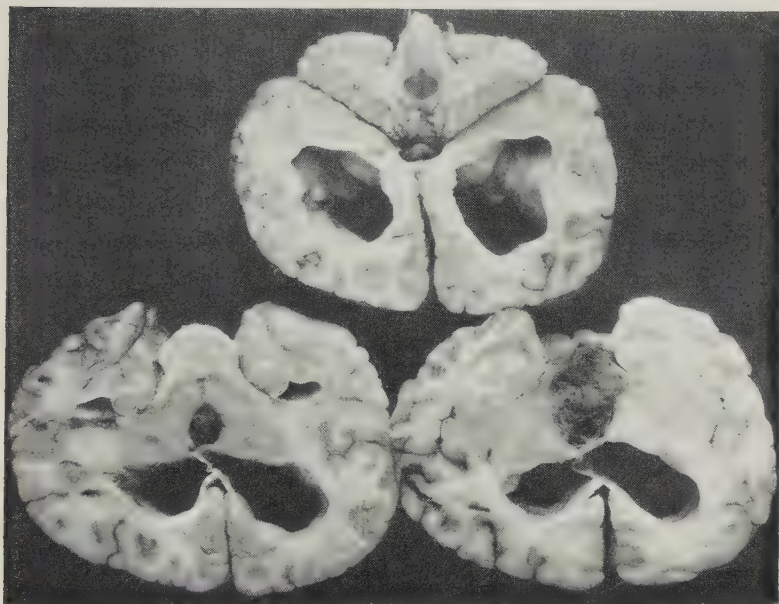


FIG. 212. Sagittal section of a tumor of the third ventricle which had produced obstruction in the anterior portion of the aqueduct.

error. Occasionally a meningioma arising from the upper surface of the tentorium may compress the cerebellum as well as the occipital lobe and give rise to cerebellar symptoms. All of these supratentorial tumors, however, have certain characteristic signs or symptoms which readily distinguish them from those lying in the posterior fossa.

Tumors arising from the midbrain or from the pineal gland may obstruct the aqueduct of Sylvius and compress the superior cerebellar peduncles and thus produce internal hydrocephalus and cerebellar

ataxia. However, paralysis of the upward movement of the eyes and loss of the pupillary light reflex are characteristic of these tumors. In those tumors arising from the pineal gland, there may be, as well, precocious mental, physical and sexual development in young males. Tumors arising in the walls, floor, roof, and choroid plexus of the third ventricle, by invasion or compression of the midbrain, may

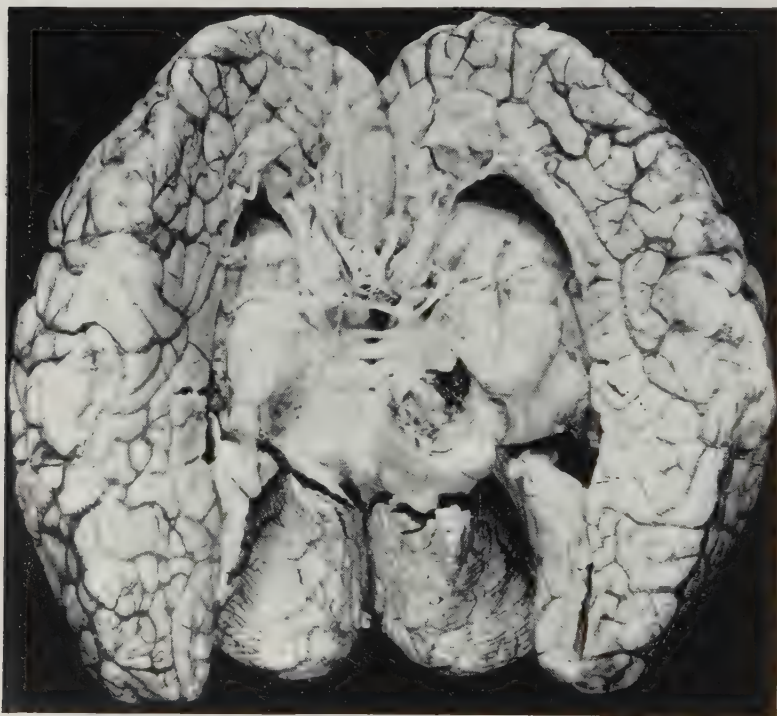


FIG. 213. An infiltrating glioma on the lamina quadrigemina

produce cerebellar symptoms. As before, the characteristic disturbance of ocular movements and pupillary reflexes obviates any mistake. Tumors lying further forward in the third ventricle may produce internal hydrocephalus from interference with the flow of cerebrospinal fluid (fig. 212) and an infratentorial lesion may be suggested. These tumors, however, tend to involve the optic tracts, and various field changes, such as bitemporal and homonymous

hemianopsia, may be produced. In these tumors of the third ventricle, lying far forward, marked diminution of vision is commonly found, out of proportion to the ophthalmoscopic changes. Supracellar cysts have been known to produce a cerebellar syndrome by the concomitant hydrocephalus and the compression of the lamina quadrigemina against the sharp edge of the tentorium. If the case is seen early enough to establish changes in the visual fields this mistake will not occur. The cerebellar signs, however, are late in appearance and

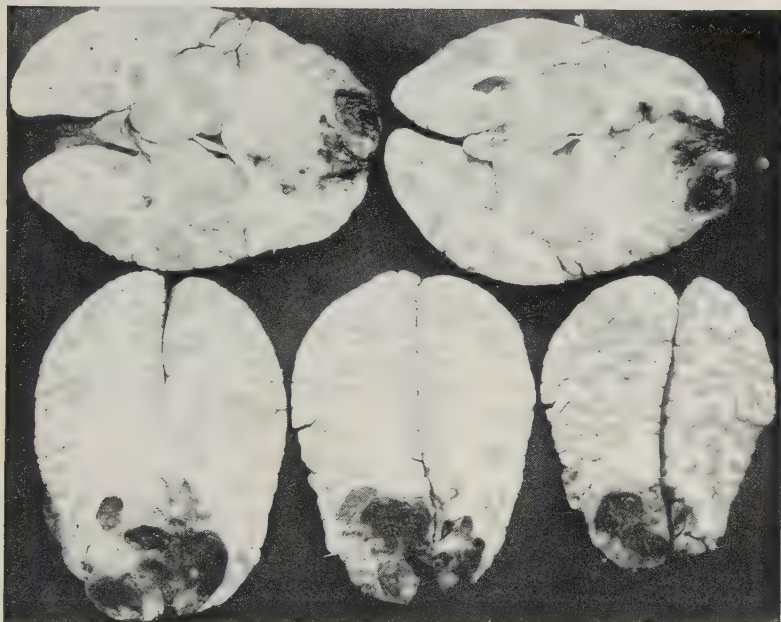


FIG. 214. Horizontal sections of a tumor of the frontal lobe producing cerebellar signs.

frequently roentgenographic studies will show calcification in the walls of the cyst and establish the site of the lesion. It is to be noticed that these tumors of the pineal gland, midbrain, third ventricle and supracellar zone all lie close to the median-line. They are deep in the brain and surgical removal is correspondingly difficult, and impossible in some cases. Accordingly, it is a matter of considerable importance to recognize their true situation and differentiate them from the more readily accessible tumors of the posterior fossa (fig. 213).

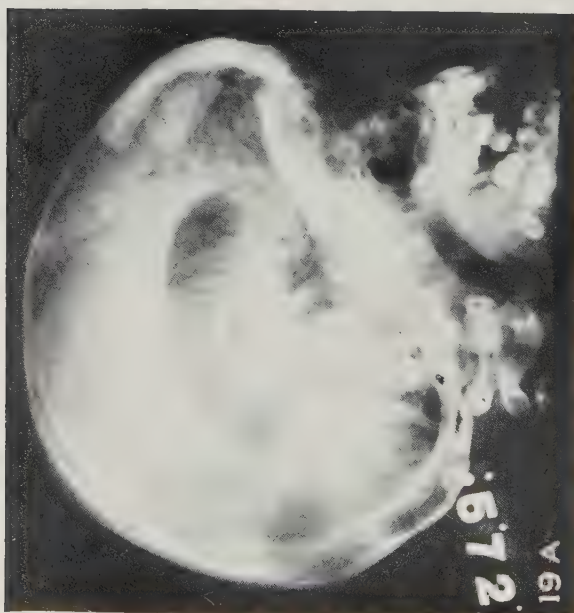


FIG. 215. Ventriculogram demonstrating the presence of air in the lateral ventricle, aqueduct, and posterior cistern, differentiating communicating hydrocephalus from an obstructive lesion of the aqueduct or fourth ventricle

Tumors of the frontal lobe occasionally produce a picture suggesting cerebellar disease and the mental changes characteristic of involvement of the frontal lobe may be absent (fig. 214). The ataxia so induced, according to some observers, has been due to interference with the fronto-pontine-cerebellar connections. Others have regarded the disturbance of gait as being not a true ataxia but an apraxia of locomotion. Whatever its nature, it has occasionally happened that the posterior fossa has been explored for tumors lying at the other extremity of the cranial cavity. Apart from the mental changes that ultimately develop occasionally in these tumors of the frontal lobe, especially those lying near the base, visual changes of the type de-

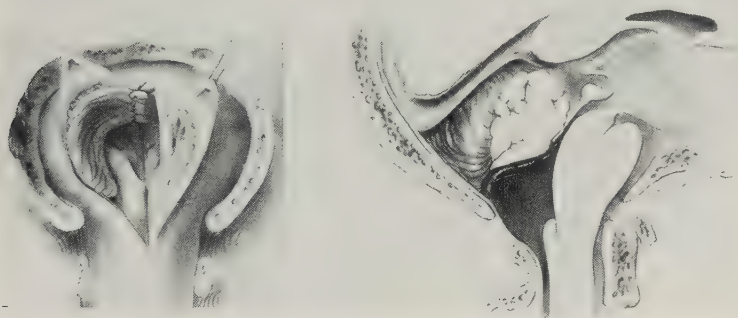


FIG. 216. Surgical illustration of circumscribed arachnoiditis with enlargement of the posterior cistern associated with communicating hydrocephalus.

scribed by Kennedy may be present and aid in localization. The visual syndrome consists of a homolateral optic atrophy and a heterolateral papilledema; there is a central scotoma on the side of the lesion and a generally contracted or normal visual field on the opposite side. Pneumographic studies may reveal an obliterated or truncated anterior horn of one or both lateral ventricles. The cerebellar signs of supratentorial, occipital meningioma are mild in comparison to other symptoms and changes in the visual fields, such as homonymous hemianopsia, appear early. The tentorium is relatively rigid and the cerebellum is not likely to be involved severely until late in the course of the disease.

Acute or chronic arachnoiditis involving the leptomeninges around

the cisterna magna (figs. 215, 216 and 217) may produce a clinical syndrome that closely resembles and may even be identical with the signs and symptoms of cerebellar tumor, especially when the latter involves the vermis. There are no reliable criteria of differentiation. In children, headache, vomiting, blindness and ataxia with internal hydrocephalus, cracked-pot percussion note and rigidity of the neck muscles may develop with or without history of infection. The cerebellar signs may be early and pronounced and differentiation im-

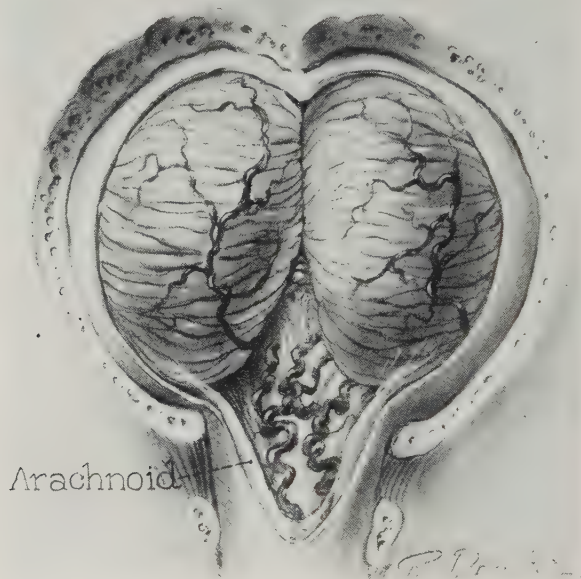


FIG. 217. Surgical illustration of an inflammatory block of the fourth ventricle

possible. Surgical exploration in most cases is the only means of differentiation and, in the face of a progressive course, is well justified. Chronic arachnoiditis involving the choroid plexus is illustrated in figure 218. Ependymitis of the aqueduct of Sylvius will produce marked internal hydrocephalus and, when this is well advanced, secondary ataxia may appear. This, however, is late and the clinical picture is perhaps more that of simple internal hydrocephalus without localizing signs than in the case of arachnoiditis. Occasionally this

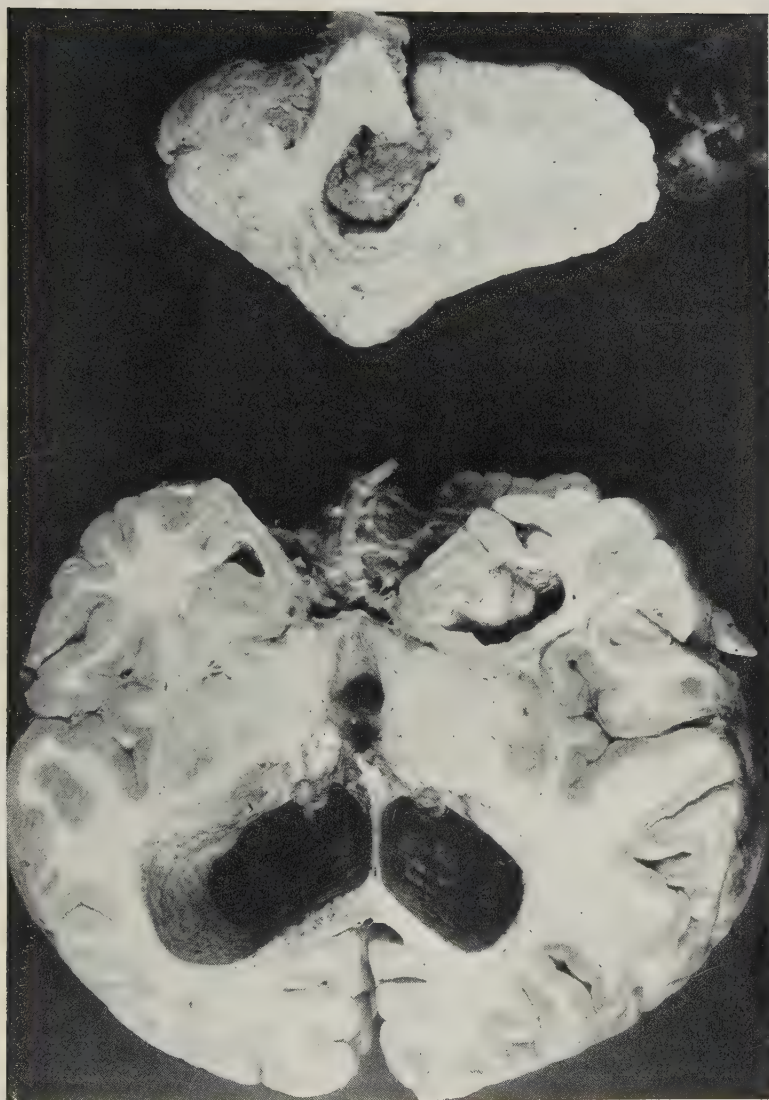


FIG. 218. Sagittal section of the cerebellum and midbrain, illustrating chronic arachnoiditis with involvement of the choroid plexus producing marked internal hydrocephalus.

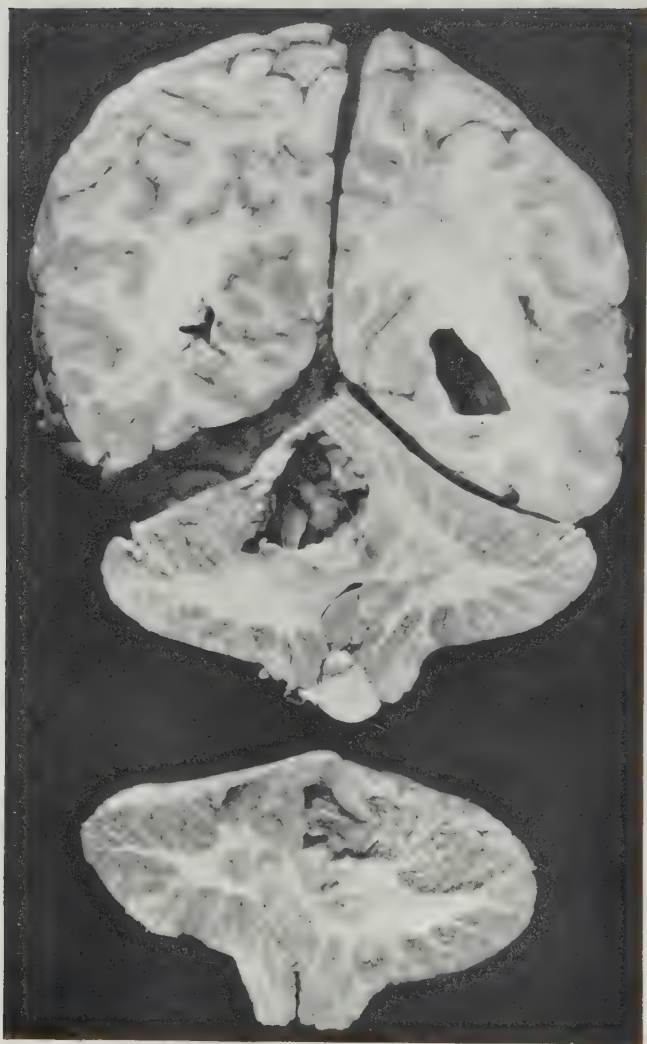


FIG. 219. Horizontal section of the cerebellum, illustrating a cerebellar abscess

internal hydrocephalus pursues a fluctuating course and the resemblance to papillomatous tumors in the third and fourth ventricles may be close.

Cerebellar abscess (fig. 219) occurring as a sequel to acute or chronic otitis media is difficult enough to diagnose in itself without the possibility of confusion with tumor having to be considered. Usually the attention is directed toward the otitic process and its complications such as meningitis and sinus thrombosis. Seldom are the signs of cerebellar inflammation as marked as those of tumor for the reason that, when the abscess reaches any size, death occurs from compression of the vital centers in the medulla.

Chronic meningo-encephalitis of the brain stem may simulate in its clinical manifestations a potine tumor, since in both cases evidence of increased intracranial pressure may be absent. A history of a general infection, such as influenza, and an irregular fluctuating course together with a high cell-count in the spinal fluid may make the differentiation possible. Syphilis, in the form of a basilar gummatous meningitis or involvement of the vessels of the brain stem, may produce a picture suggesting a tumor of the angle or pons. Involvement of cranial nerves, however, is widespread and bilateral, and the serologic tests of the blood and fluid are usually positive for the disease.

Multiple sclerosis in some of its protean manifestations and in one of its exacerbations may give rise to an almost pure cerebellar syndrome. The absence of all signs of increased intracranial pressure, the characteristic findings in the spinal fluid and the general course of the disease are enough to obviate confusion with cerebellar tumor. Loss of abdominal reflexes, motor and sensory changes confined to the lower extremities and involvement of the sphincters sooner or later appear, suggesting a disseminated lesion. Degenerative diseases of the cerebellar system, such as Friedreich's ataxia, Marie's hereditary ataxia, dyssynergia cerebellaris and the various familial cerebellar degenerations described by numerous observers seldom suggest a tumor since their course is gradual and free from all signs of increased intracranial pressure even in the presence of marked cerebellar signs. A familial history is usually present and stigmas of degeneracy support the conception of biologic inferiority.

RESULTS

Of the 215 patients operated on (175 since January, 1920) 121 are still alive; 69 have improved so that they are able to carry on useful occupations; 52 have been relieved temporarily of the symptoms of increased intracranial pressure and have been afforded palliative relief from the localized symptoms; 43 of these are helpless.

We have purposely avoided the word "cured" since there is considerable question whether gliomatous tumors, cystic or otherwise, are ever cured. Successful removal of endotheliomas and intracapsular removal of acoustic tumors might be considered to amount to cure, but frequently a vestige of the previous complaint remains, such as deafness, nystagmus or mild ataxia. Even though some mild symptoms remain or the disease should recur after a number of years, the results are well worth while and sufficient to warrant surgical treatment if the symptoms of intracranial pressure can be completely relieved and the localizing symptoms partially. The only alternative to surgical relief or temporary abatement of symptoms by means of radiotherapy is death.

POSTOPERATIVE CARE

The postoperative care in cases of cerebellar tumor is not unlike that employed in any general surgical case. A cerebellar wound is dressed either with sterile gauze and a figure-of-eight bandage with a cross over the cerebellar area, or with sterile gauze and a crinoline dressing; the latter insures firmness which prevents movement of the head on the neck. The patient is permitted to lie on either side, with a small pillow under the head, or on his chest, with two pillows under the chest and a small pillow under the head. If there has been considerable loss of blood during operation, a 5 per cent solution of glucose or a physiologic solution of sodium chloride is given rectally, by the Murphy drip for the first twenty-four hours. Water is allowed as soon as the nausea ceases after ether anesthesia, or immediately after local anesthesia. Should there be marked intracranial pressure, we advise 10 per cent or 20 per cent glucose solution by rectum, and the use by mouth of hypertonic solutions in preference to water.

The diet, which is begun on the second day, should consist chiefly of liquids and semi-solids until the fourth day, when a full diet may be given.

The patient is elevated gradually and on the fourth day after operation is allowed to maintain a semi-erect position; on the fifth day he is placed in a chair for a short time, on the sixth day he is allowed to walk, and on the tenth day he is dismissed from the hospital. The superficial skin sutures are removed on the fourth day; the dressing is removed in from ten days to two weeks. In approximately three weeks from the date of operation, the patient is dismissed from our

care. If radiotherapy is indicated, it should be administered during the third week of convalescence, and again in six and twelve weeks. If favorable results are not obtained from these courses, further irradiation should not be advised.

CONCLUSIONS

Surgical treatment in the form of decompression, partial removal, or complete removal offers the greatest relief in the treatment of tumors of the posterior fossa.

Since little is accomplished by exploration, and decompression of infiltrating tumors of the brain stem, pons, and medulla, operative treatment should be advised hesitatingly.

Apparently some tumors subside under radiotherapy and, while it is doubtful if cure is ever effected, this therapeutic measure in the form of radium or high-voltage Coolidge-tube roentgen-rays should be resorted to as an adjunct to operation, or administered alone in the inoperable group.

If relief is afforded from roentgen-ray treatment it should be repeated; if there is no relief, treatment should not be continued.

CHAPTER XXII

EXPERIENCE IN THE IRRADIATION TREATMENT OF CEREBELLAR TUMORS¹

HENRY K. PANCOAST, M.D., AND FRANCIS C. GRANT, M.D.

NUMEROUS reports have been made during the past few years of the results obtained in the treatment of brain tumors by irradiation. This method of treatment is comparatively new, but by this time a large number of cases has been treated. A sufficient time has elapsed following the treatment of a large enough group of cases for those who have been engaged in the work to offer their data for purposes of study, analysis or even criticism in a way that may be to our mutual benefit. It is only in this way that we may form any comprehensive opinion of the real merits, if any, of irradiation treatment. It is passing through the same stage of trial, varying results, unjust and just criticism and over enthusiasm that has characterized the development of irradiation therapy in many other conditions. Varying results and unjust criticism can often be traced to faulty technic and over enthusiasm is an incident of chance.

This report of cases referred from the Neurosurgical Service of Dr. Charles H. Frazier is offered as a contribution toward a collective knowledge of the subject. No unusual results are claimed and our shortcomings are fully realized and acknowledged. When viewed from a conservative standpoint, our results have been disappointing in many respects, although in many instances, surprisingly satisfactory temporary results and a few more permanent ones have created an enthusiasm that has stimulated continuance of the work. On the whole, we feel that on the basis of our own experience, augmented by that of others, that there is a very definite and important future in the irradiation treatment of intracranial neoplasms, or, at least, in some of them.

In a previous communication (1) by one of us in 1921, thirty-two cases of intracranial tumors treated by irradiation therapy were

¹ From the Departments of Roentgenology and Neurosurgery, University of Pennsylvania.

reported. All but one of these were treated by radium alone, either by implantation or external crossfire irradiation, or both combined. Since deep x-ray therapy has come into general use, in all cases treated since 1923, this has been the sole method of treatment. Our reasons for the change in technic will be discussed later. From 1914 up to the present time, we have treated 136 cases of intracranial tumors, as follows:

Pituitary tumors.....	46
Cerebral tumors.....	42
Cerebellar tumors.....	48
	<u>136</u>

As this presentation is limited to the discussion of cerebellar tumors, the other groups will be excluded, and left for future reports. The pathological analysis of the 48 cerebellar tumors was as follows:

Gliomata, infiltrating.....	10
Gliomata, cystic.....	5
Neurofibromata.....	1
Endotheliomata.....	4
Unclassified (no section taken).....	14
Tumor not found at operation, and localized for treatment on clinical evidence alone.....	12
Not operated, but treated by x-ray.....	2
	<u>48</u>

RESULTS OF TREATMENT

The following analysis shows the results of treatment of the 48 cases of cerebellar tumors:

Living.....	25
Dead (known).....	12
Cases discarded (because of lack of sufficient data).....	6
Outcome uncertain (no follow-up).....	5
	<u>48</u>

In table XXIII of cases living and dead, all the tumors classified were proven by section. A few of the gliomas were further classified as different members of the glioma group, but as many of them were not, we have classed them all as gliomata.

It must be borne in mind that the operation for a cerebellar tumor is in itself a decompression operation which must be held accountable

for some of the initial or early improvement noted in operated cases treated, and which may be responsible for the entire result which is ascribed to the subsequent irradiation treatment. For this reason and the one mentioned later in connection with depth dosage, it is quite possible that cerebellar tumors may not prove to be the best ones upon which to base our opinions in regard to the exact effect of irradiation.

TABLE XXIII
CLASSIFICATION OF CASES LIVING AND DEAD

	NUMBER OF CASES	GLIOMATA CYSTIC	GLIOMATA INFILTRATING	NEUROFIBROMA	ENDOTHELIOMATA	UNCLASSIFIED	NOT FOUND AT OPERATION	NOT OPERATED UPON
Living:								
One year or less.....	10		2		2	2	2	2
One to two years.....	2			1		1		
Two to three years.....	5		2		1	2		
Three to five years.....	2					1	1	
Five to seven years.....	4		1			2	1	
Twelve to thirteen years.....	1		1					
Thirteen years.....	1						1	
Total.....	25	0	6	1	3	8	5	2
Dead, or outcome uncertain after period stated:								
Lived less than one year.....	11	2	2			3	4	
Lived one to three years.....	7	2	2			2	1	
Lived three to five years.....	4	1				1	2	
Lived twelve to thirteen years.....	1				1			
Total.....	23	5	4	0	1	6	7	

It will be noted in the above table that all cases of cystic gliomata died, although one lived for over five years. One case of infiltrating glioma is still alive over five years and another is still living after nearly thirteen years. This last case received a heavy implantation dose into a solid tumor, which was not removed, and was subsequently treated four times up to 1920 by external radium irradiation. He has remained blind and very ataxic. In 1921, he was reoperated upon

because of a recurrence of pressure symptoms. A large cyst was found at the site of the original tumor. This was evacuated, and a section removed from the cyst wall showed no tumor tissue.

Two of the cases who died (*) (°) exhibited widespread metastasis by x-ray examination before death. They are of peculiar interest for this reason and will form the subject of a special report in the near future. One of the (°) was an endothelioma case, and the first patient with a brain tumor to receive irradiation treatment, early in 1914. She was operated upon by Dr. Frazier in February 1914, and about seven-eighths of a tumor was removed. Section showed this to be an endothelioma. She received post operative x-ray treatment in 1914, and external radium irradiation in 1915. She was fairly comfortable for two years, when the cerebellar symptoms recurred. She was reoperated upon in 1917 and a recurrence with marked extension was found. Much of the tumor was removed and radium was implanted. Subsequently four series of external treatment were given and the patient was kept fairly comfortable until August, 1926, when she was found to have developed metastasis to the lungs and died shortly afterwards.

The second metastatic case (*) had three operations, one in November, one in December, 1919, and the third in January, 1920. No tumor was found. At a fourth operation in January, 1921, a large cerebellar tumor was found and was removed fragmentarily. Radium was implanted and applied externally soon afterwards, and twice subsequently. In October, 1923, an x-ray examination to determine the cause of severe pains revealed extensive bone metastasis in the lumbar spine and pelvis. A cordotomy was performed because of the severity of the pain, but the patient died three days later. Section from the brain tumor showed glioma (medullary blastoma).

Our longest living case is, unfortunately, a useless one for statistical purposes, as no tumor was found at operation. The patient was operated upon by Dr. Frazier in 1913 for a supposed cerebellar tumor. A suboccipital craniotomy was performed. A section removed from a suspicious area showed normal cerebellar tissue. Radium was applied externally seven times from 1915 to 1920. The patient is still living, and, except for some unsteadiness in gait, is fairly healthy and comfortable. There is no reason to withhold treatment on cases such as this one simply because the tumor is not found. If there is good presumptive evidence that a growth is present, there can be no

objection to irradiation treatment given on the basis of clinical evidence. Such cases are, of course, of no value for statistics of the present day, when we are endeavoring to determine the effect of irradiation on tumor types.

GENERAL INDICATIONS FOR TREATMENT

In our original communication (1), we called attention to the fact that brain tumors are peculiarly adapted to treatment by irradiation for many reasons. They are usually comparatively slow in growth and rarely metastasize. These are two ideal conditions which are seldom encountered in malignancy elsewhere. They can frequently be removed in part and safety and the remaining portion left for

TABLE XXIV
CLASSIFICATION ACCORDING TO OPERATIVE PROCEDURES

	NUMBER OF CASES	X-RAY	RADIUM, IMPLAN- TATION AND EX- TERNALLY	RADIUM EXTER- NALLY ONLY
Tumor completely removed.....	8	4	1	3
Tumor partially removed.....	4	3		1
Tumor found but not removed.....	18	12	5	1
Tumor not found at operation.....	17	8	1*	8
No operation, tumor presumptive.....	1	1		
Total.....	48	28	7	13

* Section taken from supposed tumor showed no tumor tissue.

irradiation. This is usually regarded as meddlesome and poor surgery elsewhere in the body. The tumor may be exposed and a section taken, and if irremovable, it may be left intact for subsequent irradiation. Even if a clinically localized tumor is not found at operation, the case can still be treated, although at a disadvantage. In case the tumor is not found, temporary relief of pressure by decompression will be distinctly advantageous.

A large proportion of brain tumors can be regarded as made up of pathologically malignant cells which are frequently more susceptible to irradiation than normal cells. A consensus of opinion in regard to the radiosensitivity of different types of brain tumors is a problem which demands immediate attention in order to still further clarify

the subject of treatment indications and prognosis. This will be discussed later.

Our cerebellar group of tumors, treated on the basis of the above general indications, has been classified according to operative procedures and method of irradiation treatment as shown in table XXIV.

In the first group, in which the tumors were apparently completely removed, postoperative irradiation was administered as a preventive measure against recurrence in case every vestige of the tumor in each instance had not been eradicated. In the fourth group, tumors were found at autopsy in two cases and not found in one other case.

In groups 4 and 5, we feel that treatment was justifiable. If a tumor cannot be found at operation, or operation is contraindicated or refused, and there is strong clinical evidence that a tumor is present, we can see no harm in treating the case, and in a few instances, irradiation has been followed by marked improvement which could not be ascribed to any other cause. One is greatly handicapped by lack of knowledge of localization and pathological identity, but we know from experience that a comparatively large dose of x-rays or gamma rays can be administered through a considerable extent of brain tissue without untoward effects. In several cases of encephalitis epidemic, we have exposed a considerable area of the brain to large depth doses of x-rays with no ill effects that became apparent.

DANGERS

The possible dangers attending the irradiation treatment of brain tumors may be considered under several headings. So far as we have been able to observe, any dangers that might be encountered in the treatment of cerebellar tumors would apply also to brain tumors in general, including hypophyseal growths.

1. *Danger to the skin.* The healthy skin of the scalp will stand as much filtered irradiation as that of any other portion of the body. Dosage is based upon a skin tolerance unit of the average individual defined by experience. Fortunately marked variations in susceptibility are rather rare and cannot be considered.

2. *Loss of hair is a necessary consequence of adequate irradiation, and cannot be avoided.* It is wise to warn the patient, parents or family of this unavoidable result. The hair usually returns, but this cannot be promised or guaranteed. The eye brows and lashes are always protected by lead as a part of the advisable protection to the eye.

3. *Sloughing or delay in healing of the flap.* Neither is likely to occur where infection is not present provided the usual dosage is employed and treatment is not instituted too soon. It had best be delayed until complete healing is apparent and the flap seems to have regained its vitality.

4. *Injury to normal brain tissue.* As we have previously stated (1), the technic of irradiation therapy must depend largely upon the known ability of normal brain structure to withstand definite amounts of irradiation by any means of administration employed, based upon experience and animal experimentation. So far as we have been able to observe, no deleterious effects have been noted to follow a depth dose up to 100 per cent of a mild skin erythema dose of well filtered high voltage x-rays when slowly delivered. This applies to the optic nerves as well as normal brain tissue. Three ports of entry are usually necessary to obtain such a depth dose, although we have not yet reached it in cerebellar tumor cases.

It is probable that many brain tumors, like malignant tumors elsewhere, are quite radiosensitive, others nearly as resistant to irradiation as the surrounding normal tissues, still others are just as resistant, and possibly some are more resistant. When tumors of the last group are identified by experience, it will be known that treatment of them will be futile. Irradiation will be of doubtful or no value in the third group. In tumors of the first group, external irradiation alone should yield excellent results. In the second group, it will probably not suffice, and possibly it will be found necessary to go back to our old method of radium implantation as a supplementary procedure. Implantation may be carried out by the use of temporarily placed needles or permanent gold or platinum emanation tubes, but this incurs the added risks of infection and the destruction of normal brain substance. Such procedures will demand refinements in technic that have not yet been practiced, and the closest coöperation between the surgeon, radiologist and physicist.

It has been proven by experimental work on animals carried out in 1920 by Williamson, Brown and Butler (2) and in 1921 by Pendergrass, Hayman, Houser and Rambo (3), that normal brain tissue will not withstand very large doses of radium implantation. The destruction of comparatively small areas of normal brain was followed by death. The lesson to be learned from this experimental work is that implantations must be kept away from uninvolved brain tissue in

brain tumor cases. One must be very certain that a suspected area is brain tumor tissue before implanting needles or tubes, and their use is contraindicated when a tumor is very nearly or entirely removed.

Needles or emanation tubes, to be effectual, must of necessity be implanted somewhere near the actively growing periphery of the tumor, for their direct effect upon the cells in this portion and partly for crossfire effect upon the central portion of the tumor. Implantation doses as small as 360 mgm. hours of filtered radium caused death in dogs. The older forms of glass emanation tubes have been advised against unless implanted directly into the tumor away from the periphery, so that tumor tissue could act as a filter to protect the normal tissue. Implantations in tumors, if employed, must be carried out over an extended area and the dose must be comparatively small and supplemented by external irradiation. The tubes or needles must be carefully placed and properly distributed according to a prearranged plan and not on the spur of the moment. Obviously, implantation can be successful only in localized growths and should not be used in infiltrating tumors nor in tumors near vital centers.

5. Reactions to treatment. One should be constantly on the watch during treatment for signs of reaction due to the irradiation. This will be manifest by evidences of increased pressure, especially headache, vomiting or choking of the discs. Immediate cessation of treatment is indicated. We have found reactions are not so apt to occur since we have modified our technic. Hospitalization is advisable in all cerebral and cerebellar cases and should be insisted upon if much increased pressure exists.

TECHNIC

Our first brain tumor patient, the cerebellar endothelioma case already referred to as having died with metastasis, received x-ray therapy for the first series of applications in 1914, but was subsequently treated by radium, and from 1914 to 1923, all cases (20 of the cerebellar group) were treated by radium alone. Surface irradiation was used in every instance and was supplementary to implantation in 8 cases. Since 1923, all cases (28 of the cerebellar group) have received deep x-ray therapy alone. We believe this method is preferable to the employment of smaller quantities of radium. We would probably have no objections to the use of the radium 10 cm. pack containing a large amount of radium emanation were it available.

In our earlier cases treated by high voltage x-rays, we gave a full erythema dose to one side of the head and a half dose to the other side

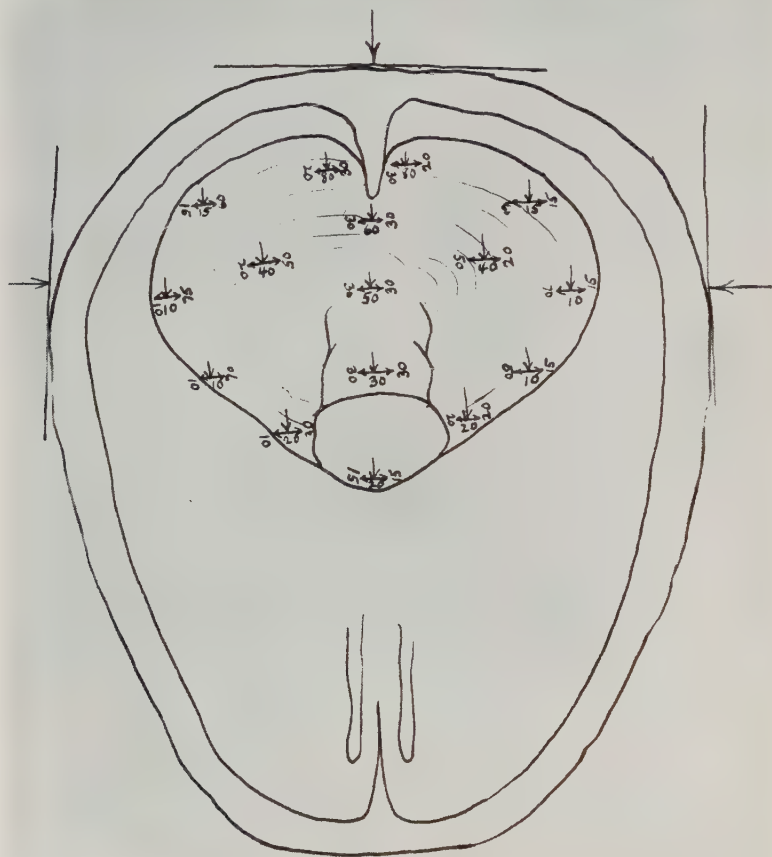


FIG. 220. Diagram showing the necessity of at least three, 6 cm. by 8 cm., ports of entry in the treatment of cerebellar lesions by deep roentgen ray therapy. For obtaining the actual depth dose at any one point, add the three percentages together.

in cerebral and hypophyseal tumors, and a single wide area over the back of the head in cerebellar tumors. Later on, a full dose was administered to each side of the head in the cerebral and pituitary

cases, but our cerebellar technic remained unchanged. Depth dose measurements showed us that we were not getting 100 per cent irradiation at tumor sites in cerebral and hypophyseal growths, and we have recently added a third port through the top of the head in order to bring the tumor site dose up to 100 per cent, or very close to it, in every instance.

Measurements in cerebellar cases showed that we were getting only 40 to 60 per cent of an erythema dose into deep cerebellar and angle tumors and 90 per cent to the posterior portions of cerebellar growths through the one posterior port of 8 by 14 cm. field. This decided us to change our technic recently to two lateral ports of 6 by 8 cm., which permits us to deliver 50 to 75 per cent throughout the cerebellar areas, except 85 per cent on each lateral aspect. We are now endeavoring to manouver a third port in order to raise this percentage still higher (fig. 220). One-half dose posteriorly would raise the dosage slightly throughout the entire cerebellar region, but possibly a 100 per cent dose cannot be reached with safety. Lower voltage x-rays will give a very much smaller depth dose and 100 per cent could never be reached by the low voltage technic.

Up to the present time our cerebellar tumors treated by x-rays have received less irradiation than the cerebral tumors, and theoretically, our best results should not have been realized in cerebellar tumors. Consequently, the effect of deep x-ray irradiation upon different tumor entities may be more accurately determined in cerebral than in cerebellar lesions. We are not prepared to state any differences in effects at this time, but the problem is being worked out.

Our previous remarks concerning radium implantation were made partly for the purpose of suggesting a possible way of increasing the cerebellar depth dose to a desired safe figure.

We have never been in sympathy with the single or rapid massive dose method of administering deep x-ray therapy, and we have never practised it in the treatment of brain tumors. It is undoubtedly dangerous. Plenty of time must be taken in treating such cases. Decided evidence of a sudden increase in pressure was exhibited in several instances when we were treating patients somewhat more rapidly than we do at the present time, and as a result, we insisted that all patients being treated should be hospitalized. We later changed our technic to a fractional dose method now being employed. Our dose to any one area is 300 milliamperere minutes, but not more

than 40 to 60 milliamperes minutes is given on any one day. Even with this slow progress, we have had to discontinue treatment temporarily in several instances. Levy (4) calls attention to this necessity, especially in connection with the appearance of choking of the discs. We have previously referred to it in reactions under the dangers from irradiation.

Another reason for adopting the modified fractional dose technic was the rather general tendency in recent years to treat all cases of malignancy by that method, with apparently better results. It is possible to give more than 100 per cent of an erythema dose through each portal if the applications are carried over a considerable time. Brain tumors must be treated according to the same principles that apply to tumors elsewhere, but, of course, with due regard to the fact that they are in the brain.

Exact localization of tumors is really to be regarded as an essential factor in the irradiation treatment, which can be carried out to far better advantage when the exact location of the tumor area is known. One cannot carry out a satisfactory plan of attack by the proper depth dose otherwise.

RADIOSENSITIVITY OF TUMORS

Next in importance to the localization of a tumor and the proper technic for its treatment, is the determination of its histological characteristics. Anyone who has had much experience in irradiation therapy of tumors elsewhere in the body, has learned that there is a considerable difference in the response of not only different varieties of tumors, but also in many that are histologically similar. Pathologists who have studied this phase of malignancy are beginning to recognize different grades of glandular and epidermoid carcinomas, for example, and from their knowledge of irradiation effects, they are able, in many instances, to prognosticate the effect of x-ray or radium therapy. This is true also in Hodgkin's disease and other lymph gland tumors. It is reasonable to expect similar variations in different forms of brain tumors and in different histological variations in the same general type of tumor. Anyone who has treated many cases of intracranial growths cannot help realizing that this is true. Bailey (5) has taken a very important step in his efforts to separate as many pathological entities as possible among brain tumors and to study and discuss the reaction of each one to irradiation.

Bailey (5) has called attention to the lack of any favorable reaction exhibited by meningiomas and acoustic neuromas, and has cited cases of gliomata which were exactly alike in anatomical location, gross appearance and general histological type, but in which irradiation produced diametrically opposite effects. There must, of course, have been a difference in the special characteristics of the cells. We have already called attention to the fact that all of our cystic glioma cases died in a comparatively short time, with one exception, as would be expected in this type of growth. The infiltrating glioma cases averaged a longer period of life. We have treated several gliomata of the orbit, and in every instance practically a caustic dose of radium was necessary to destroy the accessible portions of the growth, and the tumor has always recurred, probably from the deeply involved portion of the nerve, which was beyond the reach of the caustic dose of radium and unaffected by the external irradiation, acting as the focus for recurrence. Bailey and Cushing (6) have shown that vast histological differences and marked variations in malignancy exist in various members of the glioma group of tumors, and they have cited a few instances in which different members of the group have shown quite dissimilar reactions to irradiation.

In order to work out the problem of irradiation therapy upon a rational basis, we must carry our investigations along two lines. First, roentgenologists must agree upon a fairly uniform technic, for it is impossible to make comparisons or to compile any dependable data as long as such widely different methods prevail as at present. Second, neuropathologists and neurosurgeons must follow along such lines as are to be found in the admirable work of Bailey and Cushing (6) and others, and then they must coöperate with the radiologists in an attempt to group tumors for prognostic purposes. The treatment of brain tumors is comparatively new, and each group has been working along its own lines instead of all meeting on a common ground.

It is true that we shall have to continue always to treat some tumors without operative proof of localization, and others without the proof of identity by section, but it is hoped that the number of these will be few.

CONCLUSIONS

1. Forty-eight cerebellar tumors out of a total of 136 intracranial growths have been treated by irradiation over a period of thirteen years. Of these, 25 are known to be alive for varying periods of a few months to the thirteen years.
2. The first requisite for adequate treatment is exact operative localization. When the tumor is not localizable, the case can still be treated, but at a distinct disadvantage.
3. Uniformity of irradiation technic is highly desirable, and does not exist at the present time.
4. Radiosensitivity of different types of tumors and degrees of malignancy must be determined before we can reach any decision as to whether irradiation accomplishes any definite purpose or attempt to prognosticate results. This will be possible only by close cooperation between radiologists, neurosurgeons and neuropathologists.
5. The apparent success ascribed to irradiation therapy in cerebellar tumors may be frequently the result of the operative procedure, which is in itself a decompression.
6. It is probably not possible as a rule to administer so large a depth dose to cerebellar tumors as can be applied to cerebral and hypophyseal growths because of anatomical location.
7. We cannot speak of "cures" in connection with brain tumors with any more justification than the term is applicable to malignant growths elsewhere.

DISCUSSION

The following questions submitted to Dr. Pancoast before the Commission, together with the answers to them, are here reported verbatim.

DR. CHARLES H. FRAZIER: I think Dr. Pancoast's paper is an important one. It is probably the first milestone, as it were, in this question of radiation for brain tumors. Those of you who have followed the literature on this subject within the past two years know that the papers that have come out on the treatment of brain tumors by radiation have not contained any specific statement as to the type of tumor and no specific statement as to exactly what happened in each individual case.

I think we ought to bring up the question, perhaps, as to whether we are entitled to include in our list of successful cases; that is, cases in which radiation has proven effective, those in which they were apparently unmistakable clinical signs of brain tumor, or must we disregard and discard all those cases which are not actually verified by histological examination. Certain it is, that in everyone's

practice there are many cases which have been diagnosed and definitely entered as cerebellar or cerebral tumors, with the localization very accurately made, which have not been operated upon and in which no histological examination was made. And so it is with our series, that is a certain number of cases in which the localization has not been possible, but in which the clinical evidence seemed to be unmistakable.

I recall to mind one of Dr. Pancoast's patients, a young girl who at the time had all the earmarks of a cerebellar growth, who was absolutely incapacitated as regards her station and gait, and yet today she has improved to such an extent that she has gone to school, she is completing her education; she is in control of certain coordinated movements through which she is able to take lessons on the piano, so that to all intents and purposes she has made an almost brilliant recovery under the x-ray treatment.

Practically, the question arises as to when we regard a case as having fully recovered; what is to be our standard as to perfect cures? We are unable to see any reason, of course, in the progress of the treatment. Can we say that a case can be considered cured after the lapse of three, five, ten years, or more? May we say that a case is cured, for example, in which there is no evidence of any progress of the disease but the patient has certain stigmata, certain residual effects anyway of the destructive effects of the growth in the earlier course of the disease.

There is a good deal that we should agree upon in presenting our statistics in future, and probably five years from now we ought to be able to speak very much more positively and more definitely as to what can be accomplished, but Dr. Pancoast has done two things today, I think. He has told us that we must make a detailed statistical report, with proper follow-up results, and he has told us furthermore, what is equally important, that treatment of these cases by x-ray requires quite as specific a technique as an operation for a brain tumor. It is not fair to the patient, and it is not fair to the subject, and it is not fair to the compilation of statistics on this subject, merely to tell the patient after his operation, that he must have x-ray treatment, and then sent him off hither and yon to any one who may have an x-ray machine. That has been done in the past and a great deal of it is being done at the present time. I quite agree with Dr. Pancoast that these cases, if they are treated at all, ought to be treated with a definite standardized technique.

DR. HENRY A. RILEY: Did I understand correctly, Dr. Frazier, that the diagnosis of that tumor which metastasized to the lung was an endothelioma?

DR. HENRY K. PANCOAST: One endothelioma and one glioma.

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